ABSTRACT

Title of Thesis:	**FORAGING STRATEGIES, USE OF SPACE AND AGGRESSIVE BEHAVIOR OF DOMESTIC FOWL (*Gallus gallus domesticus)***
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Domestic fowl were tested in three experiments, all investigating the mediating effects of three group sizes of 5, 10, and 20 individuals, on behavioral responses under varying environmental conditions. The first experiment investigated social spacing and aggressive behavior in the presence or absence of cover panels. Smaller group sizes were more affected by cover panels than larger group sizes. In the second and third experiments patchy environments were used to test optimal foraging strategies. In the second experiment, smaller group sizes were more affected by patch locations than larger ones. In the third experiment birds were presented with patches varying in quality. Birds in all group sizes were able to immediately discern patch quality and preferred patches of higher quality. Despite generations of artificial selection pressure domestic fowl continue to forage optimally in patchy environments, and adopt flocking strategies predicted by behavioral ecology theory.

**FORAGING STRATEGIES, USE OF SPACE AND AGGRESSIVE BEHAVIOR OF DOMESTIC FOWL (*Gallus gallus domesticus)*

By

Erin Natalie Hoerl

Thesis 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
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Dedication

This work is dedicated to my grandfather, Arthur Edwin Hoerl Jr., that I might make him proud and do justice to his name. He was a brilliant man, and an inspiring and endearing figure in my life.

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Table of Contents

List of Tables

List of Figures

Chapter 1: Background Literature Review

Effects of Domestication on Bird Behavior

Broiler chickens have been genetically selected for increased growth, performance, and efficient feed conversion rates. Adjusted behavior strategies are not the only consequences of artificial selection. Physiological changes have occurred in domestic broilers as well. The interaction of these two factors is what enhances productivity. Compared to layer-type and wild-type jungle fowl broilers eat more, grow larger faster, and show higher feed efficiency and lower energy expenditure (Jackson & Diamond 1996).

These intense selection pressures have adjusted broilers' foraging strategy to minimize energy expenditure, through diminished physical exertion, while maximizing energy intake, through increased food consumption and efficiency. Such adjustments may be adaptive in the commercial environment where feed and water is provided free choice. Birds selected for highly efficient feed conversion spend most of their time resting and eating (Braastad & Katle 1989; Channing et al. 2001; Cornetto & Estevez 2001a; Murphy and Preston 1988; Nicol 1992; Schutz et al. 2001; Schutz & Jensen 2001). Results from the combination of inactivity and crowding include leg problems, breast blisters, and injuries from maladaptive behavior patterns, all of which negatively impact the birds' welfare.

Domestic poultry, layers and broilers, are most likely descendents of red jungle fowl (Dawkins 1989; Siegel et al. 1992). Through the years of selection for production

trait meat-type and egg-type strains have developed with markedly different physiological and behavioral characteristics. Egg-type birds are far more active, still are a 'flight risk' in production environments, and obviously have been selected for increased egg production. Therefore it is reasonable to assume that all resources are applied to ward the production of eggs. Broilers, however, have been selected for rapid weight gain. As meat-type birds, broilers are heavier than layers and display fewer and less pronounced activity levels. They are generally considered in the industry to be "lazy" and not prone to flight. Because of their selection for efficient food conversion rates they presumably direct all resources to body mass, particularly in the breast region. These enlarged breasts and overall muscle mass are certainly a contributing factor to the basic poor leg health

Katanbaf (1988) found that growing birds distribute all resources into growth. Jackson and Diamond (1996) warn however that conscious selection for production traits may have led to negative byproducts in bird health and welfare. The immunological system may be compromised as a result of allocating resources to production traits. Katanbaf (1988) showed reduced resistance to immune challenges and Rauw et al. (1998) noted reduced fertility in males and females, negative immune performance, increased rates of injury and mortality, and sensitivity to environmental stresses - concluding that growth capitalized all resources leaving the birds unable to cope with the environment.

Assessing the welfare of modern strains through comparison with wild jungle fowl may not be the most appropriate method. A departure from natural behaviors is expected in any domestic animal that must adapt and learn to strive in captive environments (Dawkins 1989; Newberry 1995). To succeed in modern environments the

behavior of broiler birds are required to adjust from that of wild-type birds. However, Ferrante et al. (2001) cautioned that animals have difficulty coping with rapidly changing industrial environments and management practices.

Jones and Hocking (1999) addressed the ability of modern science to adjust the genetic selection process for modern broiler breeder stock to include ability to cope with environmental and social stresses. The authors reported that levels of fear and social stress "respond readily to genetic selection" (p.343). Selecting birds based on their performance traits and also their ability to cope and thrive under commercial environments would improve well-being and raise the current levels of bird welfare (Craig & Muir 1998). Advances in animal breeding and husbandry have produced modern poultry strains with highly efficient performance traits. Further advances can increase animal production, but also produce healthy, well-adjusted animals.

Dominance Hierarchies and Aggressive Behavior

Aggressiveness in poultry is a goal-oriented behavior in that all agonistic behavior stems from the ethological drive to gain and ultimately control access to resources. Resources represent tangible benefits for the animal, such as feed and water, mates, perching sites, nest boxes or pen wall space. Resource control enables an animal to maximize its fitness, resulting in an increased number and quality of progeny (reviewed in Grant 1993). Through resource monopolization birds attain benefits that outweigh the cost of aggressive interactions (Brown 1964), such as energy expenditure and risk of injury or death.

The Formation of Hierarchies and their Ensuing Benefits

Aggressive behavior in poultry has been shown to decrease with formation of a dominance hierarchy, or pecking order (Syme & Syme 1979; Rushen 1982). The dominance hierarchy assures resource exploitation by dominant individuals and is maintained by occasional pecks and threats (Banks 1984; Banks et al. 1979; Stahl et al. 2001). Dominants are usually the winners of the aggressive interactions, while subordinates will lose most encounters. Dominance and subordinance is relative: status is expressed when birds encounter one another.

The exact characteristics that make a bird dominant or submissive are not completely understood. Many studies have suggested that phenotypic qualities such as comb size and body weight contribute to rankings (for review, see Syme & Syme 1979; Cloutier & Newberry 2000). Furthermore, during the formation of the hierarchy recent social experience, such as winning or losing a fight, has also been shown to have a significant impact a bird's rank (Cloutier & Newberry 2000).

All animals in the group benefit from social hierarchies (Pagel & Dawkins 1997). The most dominant animals are granted preferential access to resources without suffering retaliatory behavior, while subordinates evade further costly altercations (Rushen 1982; Banks 1984; Pagel & Dawkins 1997; Stahl et al. 2001). Both gain a level of environmental predictability; and avoid the initial cost of fighting over a resource in future encounters. Pagel and Dawkins (1997) hypothesized that social hierarchies are beneficial to all parties at small group sizes, even if the rate of resource acquisition is not increased for dominants. This

is because neither dominants nor subordinates will have to pay the cost of fighting over resources once a dominance relationship has been established.

The attempts to form a social hierarchy can be detected as early as week 2 in domestic broilers; at this point birds begin to threaten and peck at one another (Rushen 1982). However the dominance hierarchy does not become settled until after weeks 6 to 8 for females and 10 to12 for males (Rushen 1982). According to Rushen (1982) the dominance hierarchy becomes stable as birds begin to submit to aggressive behaviors, rather than retaliate. Rushen argues that the bird's final position in the peck order will depend most importantly on its individual characteristics, the age when it first started behaving aggressively, and the age at which other birds began submitting to it.

Costs and Assumptions of Hierarchy Formation

Wild Junglefowl generally maintain flocks of between 5 and 48 individuals (Collias et al. 1966). Social hierarchies have been documented in both wild and domestic bird flocks housed in natural, free-range, and small production environments (Banks et al. 1979; Mankovich & Banks 1982; Rushen 1982; Banks 1984; Gvaryahu et al. 1994; Stahl 2001). Hierarchical formation and stability is based on the assumption that birds recognize most, if not all counterparts individually and remember the outcomes of past encounters with those individuals. Only by recognizing its social position relative to other individuals can the bird behave according to the hierarchy, and thus benefit from it (Syme & Syme 1979). To benefit from the social order birds must encounter each group member on a regular basis. However as group size increases individual

identification may become difficult or even cognitively impossible at very large flock sizes (McBride & Foenander 1962; Mench & van Tienhoven 1986). Hence in increasingly large groups the dissolution of the hierarchical system is predicted. Birds may loose the cognitive capacity to recognize additional individuals and such efforts may prove too costly when birds can expect to have little contact with all flock mates (Pagel and Dawkins 1997).

A bird can only recoup the initial energy expended to form hierarchies when further aggression becomes unnecessary. If a bird fails to encounter individuals frequently, recognize them and remember the outcome of any previous encounters, hierarchies will never form and aggression will continue indefinitely. As group size increases more aggressive interactions become necessary in order to settle all possible dyadic relationships. Because of the initial cost of hierarchy formation, it will only become established when the chances of re-encountering each individual is high, ensuring recouping of the initial cost (Pagel & Dawkins 1997).

Theoretical bases for the underlying assumptions of hierarchy formation can be further explored with economic demand curves. Time spent engaging in aggressive activities draws the bird away from foraging and procurement of feed. When food and water are provided *ad libitum* for thousands of birds, the cost of defending a resource can never be recouped (reviewed in Grant 1993). Birds engaged in an agonistic encounter lose foraging time and, as their attention is directed towards one another, individuals not involved in aggression have free access to resources. At small group sizes the cost of aggressive encounters, such

as the energy expended and the risk of injury, will be outweighed by the benefits of resource monopolization and avoidance of further altercations. As group size increases net benefits peak and eventually diminish, beyond which a tolerant strategy is more energetically favorable (Estevez et al. 1997). These parabolic demand curves are not only dependent on group size but also spacing and availability of different resources, for example food, water, wall space, etc.

In experiments using small group sizes (less than 60) aggression has been shown to increase as group size increases (Al-Rawi & Craig 1975; Hughes & Woodgush 1977). Al-Rawi and Carig (1975) noted increases in aggression levels as group size increased from 4 to 28 birds. Douglis (1948) found that birds were able to recognize 27 individuals, both with permanent and transient group membership. This would suggest that birds are capable of forming dominance hierarchies at small group sizes, thus aggression should initially increase with group size increase as they attempted to do so. However beyond cognitive capacities or ethological benefits social tolerance is predicted and has been demonstrated in numerous experiments (Estevez et al. 1997; Hughes et al. 1997; Nicol et al. 1999). Hughes et al. (1997) mixed birds from a flock of 300 with either birds from a different flock, or birds from their home flock. The authors found no differences in aggression measures. Birds apparently did not recognize individuals from their own home pen and thus could not classify birds from another flock as 'unfamiliar'. No social hierarchy was attempted and birds adopted a strategy of tolerance towards strangers.

Conditions Affecting Aggression

Genetic selection, as well as the environmental and social conditions present in production settings, has a profound effect on aggression (Mench 1988; Nicol et al. 1999; Cornetto et al. 2002). Broilers (meat-type birds) have been selected for efficient feed conversion rates, rapid weight gain and increased total body weight. A genetic predisposition for reduced activity levels may aid in increasing broiler performance. Broilers do not employ energetically demanding aggressive strategies and in fact show an increase in the generally low number of pecks and aggressive threats when food is limited. Mench (1988) found fewer pecks and threats in broilers when compared with layers (egg-type birds). However this discrepancy faded once broilers were feed restricted. Increased aggression under feed restricted management has important welfare application, as this is a commercial practice within broiler breeder flocks, who are raised for breeding rather than meat purposes.

Aside from the total number of individuals in a pen, the specific number with which a bird must compete at any given time may be a contributing factor to the aggressive/defensive strategy. Estevez et al. (2002) found that the specific number of competitors present at a resource dictated the aggressive/defense tactics birds employed. As the group size at a resource increased the number of pecks delivered decreased, suggesting a switch from a competitive to a tolerant social strategy. This active switch in behavior strategy was further substantiated when the authors found consistent peck numbers after testing groups of 15 birds obtained from the larger group sizes.

When examining social effects on aggression, group size, stocking density and pen size are often confounded. These three factors can have profoundly different effects on aggressive behavior (Keeling & Savenije 1995; Carmichael et al. 1999; Nicol et al. 1999). In order to study the effect of group size investigators must choose to either maintain constant stocking density, thus increasing pen size as group size increases, or maintain constant pen size. In the case of the former, pen size varies with group size. However in both scenarios one effect is always confounded with group size and the actual effects cannot be distinguished from one another. Thus caution must be taken when examining the effects of group size, stocking density and pen size on aggression because variables are confounded. Freed (2003) designed an experiment in which all three factors were addressed and discovered that pen size, or more specifically the amount of available space per bird, was the most significant factor affecting behavior.

Nicol et al. (1999) distinguished between stocking density and flock size by comparing this experiment, in which stocking density was increased by increasing group size within a given pen with that of Carmichael et al. (1999) in which stocking density was manipulated by decreasing the pen size for a given group size. This comparison revealed increases in feather pecking when stocking density and group size were confounded, but no such increase when pen area and stocking density were confounded. Only through cross-comparison studies and through studies such as Freed (2003), designed specifically to test all three confounded factors, can the individual effect for group size, pen size, and stocking density be exposed.

Besides pen size, the distribution, type and number of resources such as food, water, nest boxes, and pen space have demonstrated significant effects on both the amount and severity of aggression (King 1965; for review, see Hughes 1980; for review, see Craig & Adams 1984). Barren environments, which are common in commercial settings, may contribute to increased aggression near resources and in the void center regions. Birds prefer to use peripheral pen space and will crowd along the walls (Newberry & Hall 1990; Keeling 1995; Newberry & Shackleton 1997; Cornetto et al. 2002). This crowding often increases the number of disturbances along the walls and may amplify the amount of aggression for desirable resting locations. By incorporating cover, in the form of panels, in home pen environments Cornetto et al. (2002) reduced the number of overall disturbances and aggressive interactions but more specifically the amount of aggression seen in the empty center space diminished.

Understanding the basic principles under which aggressive strategies operate is of paramount importance to the poultry industry. Aggressive interactions have negative impacts on both the general health and welfare of birds, but also on their production value. While broilers may demonstrate adaptation to modern production environments through adopting a high-tolerance, low-aggression strategy, the inability to form a social group, leading to constantly encountering unrecognized individuals may be stressful, and increases exposure to low-grade pecking, caused by large flock sizes and high stocking densities (Newberry & Hall 1990; Grigor et al. 1995a; Nicol et al. 1999; El-Lethey et al. 2000). Besides the obvious welfare concerns, the bird may be in a state of

elevated stress due to the inability to escape such social pressures (Gross & Siegel 1981; Dawkins 1995). Constant elevated stress levels lead to sub-optimal performance (Al-Rawi & Craig 1975; Craig & Adams 1984; Nicol et al. 1999; El-Lethey et al. 2000). If aggressive strategies can be understood and eventually controlled or manipulated through improved management practices than all parties involved will benefit, the birds as well as the poultry industry.

Foraging Theory

Optimal foraging theory predicts that those animals that choose appropriate foraging strategies for their environment, and maximize their net energetic gain, have improved chances of survival and opportunities to pass on their genes to subsequent generations. The pressure of natural selection to maximize fitness comprises the underpinnings of optimal foraging theory (Charnov 1976; Parker & Stuart 1976). Many animals forage in environments containing spatially distributed clumps of food, or patches. However, in order to maximize fitness and reach optimality animals must actively distinguish the best foraging strategies, and patches of superior quality (Lewis 1980; Alm et al. 2002; Morris et al. 2002). Optimality theory assumes that animals are able to estimate average patch quality within their environment, and that they weigh the energy required to travel among patches, seek, and forage for food (Alonso et al. 1995; Lewis 1980), and identify the energetic gain available to them from each patch (Charnov 1976; Parker & Stuart 1976). If operating under optimal foraging conditions, domestic fowl should assess the quality of a current patch relative to the average patch quality and energy expenditure required to access available resources.

11

Marginal Value Theory (MVT) describes optimal foraging in patchy environments. It predicts that in an environment with homogeneous patches birds should remain at a patch only long enough to compensate for the cost of moving to another patch (Alonso et al. 1995). If patch quality is heterogeneous, consisting of both rich and poor patches, birds should visit patches of highest quality first, depleting resources until quality reaches the average patch quality within the environment (Charnov 1976; Lewis 1980; Alonso et al. 1995).

The model predicts the convergence of foraging strategies with the optimum difference between foraging cost and gain. Birds should defend a patch from others only when the energy and time costs are outweighed by the benefits of resource monopolization (Brown 1964). At small group sizes, when energetic costs of resource defense can be recouped, birds will attempt to assert their dominance over others and exclude subordinates from sharing in resources (Banks et al. 1979; Banks 1984). When group dynamics are incorporated with the optimal foraging model, strategies of individuals within the group may differ from one another as a function of dominance status (Caraco 1981; Clark & Mangel 1984; Caraco et al. 1989; Stahl et al. 2001). Stahl et al. (2001) documented that the subordinate birds in wild arctic barnacle geese (*Branta leucopsis*) flocks were located along the front edges, traveling at a faster pace and foraging more quickly than the dominants foraging along a front behind them. However once subordinate birds uncovered resources dominant individuals rushed in and excluded other birds. The foraging strategies seen in these flocks opposed one another, with subordinates attempting to move ahead of dominants and consume discovered resources before being ousted. Caraco et al. (1989) compared the foraging strategy of single versus

paired juncos, *Junco hyemalis*, in patchy environments. This study corroborated the results from Stahl et al. (2001) in that dominant individuals expelled subordinates from their discovered resource patches, causing them to adjust their foraging strategy. Despite the obvious advantage to dominant individuals, various models and supporting studies have demonstrated the unapparent benefits to subordinates.

Clark and Mangel (1984) developed a model of flock foraging behavior to demonstrate the benefits of staying in a group for subordinate birds. Individuals foraging in groups constantly monitor the foraging results of other group members and share in any information, or resources, gleaned. The collective information gained by being within a group surpasses that which is available to any single individual, subordinate or dominant. While a byproduct of low social status is delayed access to resources, subordinates in fact gain from this predictable circumstance (Pagel & Dawkins 1997). The initial energy lost during the formation of a pecking order, or dominance hierarchy, is recouped when birds no longer contest over subsequent resources. Thus subordinates not only benefit from group membership through an improved foraging rate over solitary foraging, but also benefit from the social hierarchy in that further aggression over discovered resources is avoided, as would not be the case if solitary. However one caveat of group membership and social hierarchies, if they are to benefit foraging strategy, is that individuals must recognize each other – which may not be possible under modern production practices (McBride & Foenander 1962; Mench & van Tienhoven 1986).

Environmental factors may not be the only way domestication alters foraging strategies for domestic fowl. Domesticated animals under intense artificial selection for high production traits behave in a more energy-conservative fashion than those not under

such pressures (Gustafsson et al. 1999; Andersson et al. 2001). These changes have been demonstrated by comparing the foraging strategy of wild-type red jungle fowl to that of domesticated birds, and also by comparing the foraging strategies of different strains of domestic chickens selectively bred for different production traits (Braastad & Katle 1989; Andersson et al. 2001; Schutz et al. 2001; Lindqvist et al. 2002). Jungle fowl are presumed to be the ancestor to modern strains of domestic fowl (West & Zhou 1989; Siegel et al. 1992) and thus provide a basis for comparing behavior strategies (Dawkins 1989; Siegel et al. 1992). In repeated experiments wild-type birds spend a lower proportion of time eating from a readily available source, preferring to forage for their feed (Schutz & Jensen 2001). Jungle fowl adopt a more energy-demanding foraging strategy and engage in more contrafreeloading behavior than domestic chickens (Schutz & Jensen 2001; Schutz et al. 2001; Lindqvist et al. 2002). Contrafreeloading is a foraging strategy for which an animal actively chooses to work for food when the same reward is readily available without additional work required. Bizeray et al. (2002a) noted the reluctance of domestic birds to forage for food when other resources were readily available.

Contrafreeloading, and its prevalence among various wild species (for review see Inglis et al. 1997), suggests that the mere consumption of food is neither the sole motivating factor nor the sole benefit of foraging behavior. The animal can be said to gain as much from the mere act of foraging, in the way of information about its environment, as it does from actually feeding (Hughes & Duncan 1988; Linqvist et al. 2002). Energetically expensive behavioral strategies such as contrafreeloading are only maintained in the wild if they offer valuable benefits, such as providing crucial

14

information or enabling a critical interaction with the environment. If, in the wild, predation is the most important variable in determining patch quality then contrafreeloading may offer detailed environmental information vital to avoid predation, such as the availability and proximity of suitable cover (Arcis & Desor 2003). However, if the risk of starvation is an animal's most critical pressure then contrafreeloading would provide necessary information about patch quality and habitat variability in an uncertain environment (Linqvist et al. 2002). This knowledge would prevent the animal from starving when abundant food sources or rich patches become scarce.

While environmental conditions and selection pressure have changed the behavior of domestic fowl, their behavior has often remained intact. The risk of predation has been eliminated in modern production environments, relaxing natural selection pressures present in the wild. However domestic fowl consistently behave according to anti-predator strategies and show vigilance, flocking and other fear responses in captive environments (Gvaryahu et al. 1989; Jones & Waddington 1992; Nicol 1992; Newberry & Shackelton 1997; Schutz et al. 2001). These behavioral responses necessary for survival when encountering a predator have not been eliminated from the domestic fowl's behavioral repertoire. Modern production environments have also eliminated the risk of starvation. The production industry standard is the provision of *ad libidum* food, with the main exception being the restricted feeding regime for domestic broiler breeders which are required to grow more slowly in order to improve reproductive fitness (Mench 1988). Given the relaxation of the two most likely selection pressures benefiting contrafreeloading strategies, in a situation where maximum weight gain and energy

conservation is extensively selected for over generations, not surprisingly, such energetically demanding behaviors will be reduced.

While domestic fowl display quantitatively less overall active behaviors when compared with their more wild relatives (Schutz et al. 2001) they have been shown to choose patches according to the work required and optimally forage under the principles of marginal value theory (Andersson et al. 2001). Some studies have examined the effects of increased distance between patches (Andersson et al. 2001) as well as the effects of increasing manipulation time by mixing food rewards with litter or wood shavings (Lindqvist et al. 2002). However, birds were trained prior to testing, and were acclimating to the testing procedure (Andersson et al. 2001; Schutz et al. 2001; Lindqvist et al. 2002) and possibly able to anticipate the provision of different quality patches. None of these studies examined the mediating effects of group size on foraging strategy, as all birds were either isolated for testing, or tested in pairs.

By examining the foraging strategy of domestic fowl in patchy environments, but also under various resource distribution scenarios, investigators can gain a better understanding of the foraging decisions birds make in production settings. These foraging decisions have important relevance to production, because the variation among bird weights will be high, and bird welfare (Wiepkema & Koolhaas 1993). Further investigation into the mediating effects of flock size on foraging behavior, both at small, large, and intermediate group sizes will discern the specific effects of social environment on foraging.

Use Of Space

Many environmental factors influence how domestic birds use available space, some of which have been previously alluded to and briefly mentioned in this manuscript. Social factors such as stocking density and group size (Banks 1984; Keeling & Duncan 1991; Zhou & Stricklin 1992; Keeling 1994; Estevez et al. 1997; Carmichael et al. 1999), as well by physical factors such as pen size (Stricklin et al. 1979; Hughes 1980; McBride & Craig 1985; Newberry & Hall 1990) resource distribution (McBride & Craig 1985), and age (Hughes 1980; Newberry & Hall 1990; Newberry & Shackleton 1997; Cornetto & Estevez 2001b) significantly impact movements. The effect on an individual's use and distribution pattern often results in an alteration of the total area utilized collectively by the birds or the combined home range.

When social hierarchies affect the use of space in domestic fowl, generally at smaller group sizes, dominant individuals control space nearer to the food resources (Banks 1984, reviewed in Grigor et al. 1995a). Dominant individuals monopolize these attractive pen areas and frustrate the attempts of subordinates to gain access to those areas. When investigating the behavior of laying hens, Gibson and Dunn (1985) suggested that dominant individuals enjoy a greater freedom of movement than subordinates. Dominants move around the pen freely, unchallenged by subordinate individuals; thus gaining access to all areas and settling more frequently in the most attractive areas. Conversely, as subordinates navigate the pen area they can be challenged by dominants; in order to avoid confrontations subordinate individuals will avoid dominants and thus limit their freedom of movement around the pen, demonstrating diminished use of attractive areas (reviewed in Grigor et al. 1995a).

As group size increases the formation of a dominance hierarchy becomes unprofitable. McBride and Foenander (1962) predicted that at large group sizes birds will remain in specific areas of the available space where they will form subgroups and within these subgroups establish a hierarchical social system. Therefore, the combined effects of social dominance and large group size would limit use of space. This theory assumes that birds attempt to form dominance relationships with each encountered individual through aggressive interactions, and that such interactions are both costly and stressful. Attempting to diminish stress and energy expended during costly encounters, the authors concluded that birds would restrict movements to a small range, functionally creating numerous territories within the available space. By remaining within a territory birds develop a local hierarchy with the other resident individuals and are able to avoid encounters with strangers. This hypothesis, however, has not been supported in recent studies (Newberry & Hall 1990; Estevez et al. 1997; Carmichael et al. 1999; Channing et al. 2001).

Newberry and Hall (1990) found that birds did not stick to well-delineated home sites, or territories, but rather continually mingled within the space. Estevez et al. (1997) also found that birds did not restrict their movements to specific territories within the pen, but rather were recorded at various locations across the entire pen. The amount of pen space used by focal individuals did not change with increasing group size. Again this finding directly contradicts the predictions of McBride and Foenander (1962) in that individuals from groups of 200 did not use less of the available pen area than birds in groups of 50, as would be predicted if birds were attempting to avoid unknown individuals. While social hierarchies have a significant effects on bird movement at

small group sizes, similar effects are not well-supported at large group sizes. This discrepancy suggests that the effects of group size are independent of the effects of social hierarchies. In large group sizes the physical barriers created by high stocking densities and/or large numbers of individuals, limit movement rather than social interactions occurring between flock members. This exact hypothesis was tested by Freed (2003) in which bird models, appropriately sized balls, were used to simulate the presence of other individuals while removing any possible social effects. It was the mere presence of these models that limited bird movement and available space, in the absence of any possible social interactions.

While many studies have examined the behavioral effects of stocking density, group size and pen size they are not independent of one another. Inexorably, when comparing two parameters, for example stocking density at constant group sizes, the third parameter, in this example pen size, must be manipulated with stocking density. Any interpretation of the effects of stocking density are not independent of pen size which must be decreased when holding group size constant, thus confounding the effects of stocking density with pen size. The only study, to my knowledge, which has simultaneously explored the independent effects of all three environmental factors, is that of Freed (2003). Thus any interpretation of the effects of group size must take into considerations the confounded effects of either altered pen size or stocking density, and the same is true when examining stocking density and pen size.

With this caution in mind, studies have demonstrated behavioral effects of group size, pen size, and stocking density (Nicol 1987; Keeling 1994; Estevez et al. 1997; Newberry & Hall 1997; Carmichael et al. 1999; Channing et al. 2001). Estevez et al.

(1997) found no difference in the amount of pen space used by broilers from pens of identical size. The authors suggest that pen size and stocking density, rather than group size, limits the amount of space a bird uses. Channing et al. (2001) examined the effect of group size on laying hens, while holding stocking density constant, thus increasing pen size with group size. The authors found that birds in all group sizes used an equal percentage of available space, however both the minimum and maximum neighbor distance increased with group size. The authors caution against a possible increased potential for, and incidence of crowding at larger group sizes. Newberry and Hall (1990) examined pen size, rather than group size per se with broilers, but in doing so maintained constant stocking density by manipulating group size. The authors found increased use of the total available pen space with increasing pen size, and consequently increasing group size. Keeling (1994) and Carmichael et al. (1999) investigated the effects of stocking density in laying hens, however stocking density effects were confounded with pen size, which decreased in order maintain a constant group size. Birds adjusted their time budgets under spatial restriction, limiting the activity of certain behaviors, such as walking and ground pecking, which require a larger amount of space than standing, which became a filler behavior (Keeling 1994). These results are similar to those found by Carmichael et al. (1999); birds decreased their movement and increased standing when stocking density increased but group size remained constant. The authors concluded that the proportion of birds moving was least at the largest stocking density because of the adverse effects crowding has on movement. Similarly Nicol (1987) examined the effect of cage size while maintaining constant group size, thus increasing stocking density with cage size and confounding the two effects. Birds in restricted cages

20

rested, sat, and pecked more often than birds from larger cages, which ate more and stretched more often than restricted birds (Nicol 1987). There were pronounced, and immediate, behavioral changes when restricted birds were moved to large cages; they stretched and flapped their wings more often than birds reared in spacious environments.

When comparing results from many studies, stocking densities, pen sizes, group sizes, and housing conditions often vary from one to another leading to a wide variety of experiment conditions. Estevez et al. (1997) made use of pens $10.5m^2$, and stocking densities of 4.8 birds/m^2 for 50 birds, 9.5/m^2 for 100 birds, 14.3/m^2 for 150 birds and 19.0/m^2 for 200 birds. These stocking densities are similar to those in Carmichael et al. (1999), of 9.9 birds/m^2, 13.5/m^2, 16.0/m^2 and 19.0/m^2. However in Carmichael et al. (1999) a perchery housing system with a constant height and width of 4.4m, but various lengths from 4m to 7.2m, was utilized in order to create the various stocking densities with 300 birds in each system. Channing et al. (2001) used this same perchery system, however birds were maintained at a relatively high constant stocking density of 18.5 birds/m^2, while group size increased from 323 to 912 birds. Newberry and Hall (1990) maintained a constant stocking density of 7.5 birds/m^2 for 3040 birds housed in a $407m^2$ pen, as well as for 1520 birds in a $203.5m^2$ pen. Keeling (1994) housed three birds in pens ranging from $1.3m^2$ to $0.42m^2$, creating stocking densities from 2.3 birds/m^2 to 7.1 birds/m^2. Nicol (1987) housed hens in similarly small group sizes, but in battery cages ranging from $0.85m^2$ to $2.3m^2$, with stocking densities of 7.1 birds/m^2 to 2.6/m^2 respectively. The results from these different studies complement one another despite differences in experimental conditions. Pen size was experimentally increased in all studies except Estevez et al. (1997), in which pen size was controlled and stocking

density and group size were increased. From the studies reported, general behavioral trends can be distinguished as pen size increases; the total amount of area used by the birds also increases (Newberry & Hall 1990; Carmichael et al. 1999), even when area occupied per day does not change (Newberry & Hall 1990), and distribution throughout the available space does not change (Channing et al. 2001). The additional finding by Estevez et al. (1997) that group size is not the significant factor affecting the use of total available space, when birds are housed at constant pen size suggests that it is that pen's size, as well as the stocking density, that most substantially influences the amount of space a bird utilizes.

Many studies have demonstrated the beneficial effects environment enrichment has in promoting an increase in the overall use of available pen space, as well as to distribute birds more evenly (Newberry & Shackelton 1997; Kells et al. 2001; Cornetto & Estevez 2001b). Void, predictable environments, such as current commercial poultry houses, offer domestic fowl little stimulation, and may affect their welfare and ultimately their productivity (Mench & van Tienhoven 1986; Wemelsfelder 1993; Wiepkema & Koolhass 1993; Mench 1998). Typically birds congregate along pen walls, decreasing the amount of central area occupied and increasing disturbances and aggressive interactions in highly contested areas (Newberry & Hall 1990; Newberry & Shackelton 1997; Cornetto et al. 2002). However by incorporating cover, in the form of panels, bird numbers decreased along pen walls and increased around the provided cover panels (Newberry & Shackelton 1997; Cornetto & Estevez 2001b). Furthermore aggressive interactions decreased, as did the number of disturbances (Cornetto et al. 2002).

How domestic animals use the space available to them is paramount in understanding their adaptations to current production environments (Keeling 1995). Welfare and productivity can be improved through better understanding of animal behavior and the stimuli that inhibit, as well as those that elicit, natural behavior patterns (Craig & Adams 1984; Keeling 1995).

Environmental Enrichment

The number of different definitions for environmental enrichment are only surpassed by the multitude of types reported in the literature. It has been defined by physical change that leads to increasing: biological relevance to the animal (Newberry 1995), spatial complexity (Cornetto & Estevez 2001a), exploratory behavior (Mench 1998) and environmental challenges (Wemelsfelder & Birke 1997). Research has shown that environmental enrichment improves performance (Gvaryahu et al. 1989; Bell et al. 1998; Jones et al. 1980) modifies and enhances behavior patterns (Bizeray et al. 2002a; Cornetto & Estevez 2001a), stimulates activity (Kells et al. 2002), reduces aggression and disturbances (Cornetto et al. 2002) and mortality (Gvaryahu et al. 1994), and decreases fear responses (Nicol 1992; Jones and Waddington 1992; Jones 1982; Reed et al. 1993). Enrichment can include the provision of basic items such as nest boxes, dust bathing materials, perches or cover, but can also include commercial pecking devices and other such novelties designed to promote exploratory or foraging behaviors.

Newberry (1995) limits the definition and application of environmental enrichment based on the biological relevance to the animal. Enrichment is distinguished from the mere provision of novel items in that the item or environmental change must

improve the biological functioning of the animal. Mench (1998) in turn defines two types of environmental enrichment, those that satisfy strongly motivated, high priority behaviors and those that stimulate information-seeking behaviors. The complex and variable qualities of natural environments predict a motivation to seek complexity and novelty in order to satisfy information gathering drives (Mench 1998). Barren environments may foster frustration, boredom or stress related behaviors that are often expressed through feather pecking, cannibalism, or pacing. Many investigators have studied the myriad of deleterious effects barren commercial environments may foster, such as the destructive redirection of natural behaviors towards pen mates in the absence of appropriate outlets (Gross 1983; Mench & van Tienhoven 1986; Dawkins 1988; Wemelsfelder 1993; Wiepkema & Koolhaas 1993; Wemelsfelder & Birke 1997; Mench 1998; Newberry 1999).

The modern commercial poultry production environment may sabotage bird welfare and performance because of its barren nature, lacking in complexity and stimulation. Under these conditions maladaptive behaviors such as feather pecking and cannibalism may develop, which may negatively impact both welfare and productivity (Aerni et al. 2000; Dawkins 1988; El-Lethey et al. 2000; Gvaryahu et al. 1994; Newberry 1995; Wemelsfelder & Birke 1997; Wemelsfelder 1993). Welfare may deteriorate due to boredom or frustration resulting from constant, unchanging and under-stimulating environments (Gross 1983; Bell et al. 1998; Dawkins 1988; McBride & Craig 1985; Newberry 1999). Recently, environmental enrichment has been examined as a preventative measure to decrease or inhibit destructive behaviors. Mench et al. (1998) acknowledged that successful enrichment devices improve health and physiology,

increase the range of normal behaviors, diminish abnormal or stereotyped behaviors and/or improve an animal's ability to cope with stresses.

Newberry (1999) found that domestic fowl had a strong drive to seek out novelty and challenge. The thwarting of these motivations may lead to boredom or frustration. Mench (1998) and Pettit-Riley and Estevez (2000) discussed the importance of exploratory behavior and control over the environmental, respectively, and the possible uses of environmental enrichment towards those ends. Wiepkema and Koolhaas (1993) suggest that some environmental unpredictability, in the form of novelty or exploratory opportunities, is necessary to avoid boredom. Early experience, either in a poor or enriched environment, exerts a profound affect on the animal's later behavioral repertoire and ability to cope with stressors (Jones and Hocking 1999). Wemelsfelder and Birke (1997) include environmental challenge, the dynamic conditions of an animal's environment requiring interaction and responses, as an integral component for behavioral well-being. The lack of environmental challenge has a substantial impact on bird well-being. The authors discuss the key role of environmental control in stress management, brain development and behavioral plasticity. Wemelsfelder (1993) suggests that increased stereotypies seen in modern poultry reared in barren, intensive housing conditions indicate the impairment of species-typical behaviors, and ultimately denote suffering for the animal. Gross (1983) found that in barren environments such as cages, birds had reduced immune function as well as basic lethargy and diminished weight gain relative to floor-kept birds.

While the lack of environmental enrichment and complexity may lead to impaired welfare, their inclusion is not strictly preventative; many authors have reported high

performance and carcass quality and improved well-being (Gvaryahu et al. 1989; Bell et al. 1998; Jones et al. 1980). Jones and Waddington (1992) investigated the effects of early environmental enrichment on fear responses of layer chicks later in life. In all trials birds reared in enriched environments demonstrated less freezing, more approach and investigating behaviors as well as increased vocalizations and shorter emergence times from a novel area. The authors theorized that early enrichment enhanced the chicks' abilities to adapt to subsequent environmental stressors, and reduced the frightening properties of novelty. Nicol (1992) found lower tonic immobility duration and higher general home pen activity levels in laying hens that were given access to perches and novel items to investigate. Reductions in fear responses will decrease the likelihood of exaggerated fear responses like hysteria which lead to injuries, heart attacks, increased susceptibility to heat stress and overall high levels of stress (Hughes 1980; Jones 1982; Jones & Waddingto, 1992; Nicol 1992; Reed et al. 1993; Mench 1998).

Reed et al. (1993) noted decreased carcass quality in caged layers due to significantly more strikes against the cage, causing broken bones during depopulation in birds without enrichment objects compared to those provided enrichment. Environmental enrichment, in the form of multiple small easily manipulated items, has demonstrated a growth-stimulating effect in broilers through improved body weight gain and feed conversion rates (Jones et al. 1980). Gvaryahu et al. (1989) found significant improvements in feed conversion and body weights of meat-type birds given a small imprinting object and small, easily manipulated enrichment devices. In addition Gvaryahu et al. (1994) found improved egg production and decreased mortality rates in

laying hens given access to commercial enrichment devices designed to increase pecking and bird-object interactions.

Increasing environmental complexity breaks up monotonous floor space. Not all of the available space is utilized, and enrichment in the form of cover and perches has the effect of spreading birds more evenly throughout their enclosure (Hughes & Elson 1977; Newberry & Shackleton 1997; Cornetto & Estevez 2001b). Cornetto and Estevez (2001b), Cornetto et al. (2002) and Newberry and Shackelton (1997) were able to encourage more even dispersion across pen floors both in broilers and layers, and thus decreased both aggressive interactions and large aggregations by introducing cover, in the form of panels. Hughes and Elson (1977) provided broilers with perches, and noticed an improved distribution in the pen, but also a reduction in the number of disturbances. When Cornetto and Estevez (2001a, 2001b) incorporated panels in home pens, aggressive interactions as well as the number of disturbances decreased. When moving about the pen broilers choose the most direct path, often directly over, rather than around, conspecifics; stepping on other birds can often lead to injuries. Disturbances caused by birds aggregating at pen walls may decrease carcass quality because of scratches and bruising. Even distribution created by enrichment would improve production.

Increasing motor patterns and general activity, as well as behavioral repertoires and plasticity in poultry are important goal of enrichment. Modern broiler strains spend the majority of their daytime resting (Cornetto et al. 2002). These prolonged periods of resting may have adverse effects on bird health through the appearance of lesions and sores as well as hock and leg burns from prolonged period on wet litter (Søresen et al. 2000). Leg problems are a major concern in the broiler industry; a 1993 survey of

commercial broiler production companies estimated that the incidence of leg deformities and lameness cost the industry between $80 and $120 million dollars annually (Morris 1993). This inactivity may be the result of leg problems that make movement and activity painful. However genetic selection for rapid weight gain and large body size significantly contribute to the incidence and severity of leg deformities (Craig & Muir 1998; Rauw et al. 1998; Jones & Hocking 1999; Bokkers & Koene 2003). Incorporating enrichment designed to increase exercise, such as barriers or perches, has been shown to improve bone conditioning (Rau et al., 1998; Su et al., 1999; Sørensen et al., 2000; Bizeray et al. 2002b). These improvements will in turn reduce mortalities and culling percentages related to leg problems (Morris 1993).

Birds appear highly motivated to seek and use available forms of cover and perform more comfort behaviors and use more available space (Newberry & Shackleton 1997; Cornetto & Estevez 2001b; Kells et al. 2001; Estevez et al. 2002). By providing birds with straw bales in commercial houses Kells et al. (2001) noted a decrease in resting periods, an increase in locomotion and also longer bouts of activity. Bizeray et al. (2002a) found comparable results after increasing environmental complexity by incorporating small barriers. These barriers stimulated a greater variety in motor patterns. Birds used barriers as perches, demonstrating adaptive use of incorporated environmental complexity and diversification of behavior patterns. Newberry and Shackleton (1997) provided young layers with panels to increase cover and noted that birds often perched on top of the panels as well as positioned alongside them in large numbers.

Cover and perches have obvious biological relevance to birds. In wild environments, birds would use tree branches and bushes for roosting and to seek protection from predators and aggressive flock-mates. In poultry houses birds are often kept on large open floors, with no option to perch or seek cover. Crowding seen along pen walls may be an attempt to seek the only available cover (Newberry & Shackleton 1997; Cornetto & Estevez 2001b). These studies demonstrate that birds spend a disproportionate amount of time near pen walls and Kells et al. (2001) noted that in addition to walls birds clustered around support poles when available. These behaviors are evidence of a strong behavioral drive to seek cover and protection, which is minimally provided in commercial settings.

There are a variety of theories about practices relating to welfare requirements, behavioral needs and appropriate levels of stimulation, enrichment, and complexity for domestic fowl. There are also a variety of definitions for welfare, suffering and behavioral needs. Hughes and Duncan (1988) determined that birds are significantly more motivated to perform certain behavior patterns, and frustration results from the birds' inability to perform them. Dawkins (1988) cautioned that suffering should only be declared when motivation unable to be fulfilled is prolonged or intense. Further investigation into the effects of environmental complexity and its lack thereof are necessary to improve both welfare and production. These factors must be carefully studied and seriously considered to better design suitable housing conditions.

Chapter 2: Use of Space, Social Spacing and Aggressive Behavior Under Varying Levels of Environmental Complexity

<u>Abstract</u>

The effects of cover panels designed to increase the level of environmental complexity in a testing arena were compared across three group sizes, five, 10, and 20 individuals per group of domestic fowl. Animals were tested under three environmental scenarios, either in an empty control arena, with one long panel, or with four panels equal in total length to the one long panel, representing increased environmental complexity. Environmental complexity had a more pronounced effect on smaller group sizes. Larger groups occupied more of the total pen space, but the use of space by individuals (core areas) did not vary with GS. The total core area occupied by group members increased with group size. Overall aggression was low, but groups behaved differently in each of the environmental conditions. Because birds were transported from their communal home pen environment to the testing arena, individuals demonstrated the capacity to immediately adapt to a new environment. Domestic fowl not only responded to the different physical environmental features but their behavior was markedly affected by group size, despite common home backgrounds.

Introduction

The management and housing conditions for domestic fowl offer little in the way of natural environmental features possessing historical and biological, relevance. Most specifically this refers to the absence of concealing cover, a fundamental element in wild habitats (Gray et al. 2000; Jensen et al. 2003). Newberry and Shackelton (1997) defined cover as a structural feature of the environment that enables animals to conceal themselves from predators or the aggression of conspecifics. The presence of suitable cover is one of the most crucial elements in distinguishing suitable wild environments (reviewed in Lima & Dill 1990) and plays a key role in foraging decisions (Elton 1939; Jensen et al. 2003). The presence of cover is a salient influence on domestic animal behavior and this influence has endured the process of domestication. Evidence of the effect of cover is the persistent fearful reactions of domestic fowl to actual and supposed predators (Gvaryahu et al. 1989; Jones & Waddington 1992; Nicol 1992; Newberry & Shackelton 1997; Schutz et al. 2001). The lack of suitable cover in the agricultural production system may negatively impact domesticated fowl and contribute to stress and abnormal behaviors such as stereotypies (Newberry & Shackelton 1997).

Because the fear of predation continues to shape the behavior patterns of domestic fowl (Keeling 1995) the availability of cover, or lack thereof, has been shown to significantly influence the way flocks use the space available to them (Newberry & Shackelton 1997; Cornetto & Estevez 2001a). In barren environments birds disproportionately cluster along pen walls (Newberry & Hall 1990) or any notable environmental feature, such as roof support poles (Kells et al. 2001). This clustering decreased the amount of central area occupied and increases the potential for disturbances

and aggressive interactions (Newberry & Hall 1990; Newberry & Shackelton 1997; Cornetto et al 2002). Newberry and Shackelton (1997) as well as Cornetto and Estevez (2001b) incorporated panels providing cover. Both examined the behavior of domestic fowl and found that the number of birds along pen wall decreased as animals distributed more evenly throughout the enclosure. In both studies animals showed a high degree of motivation to seek and utilize the provisioned cover. Kells et al. (2001) found that in empty chicken houses animals crowded around the only elements available, structural support beams. By increasing the level of environmental complexity with panels, Cornetto et al. (2002) reported an effective decrease in aggressive interactions and disturbances. The welfare of domestic animals housed in intensive production environments has come under public scrutiny as of late (Mench & van Tienhoven 1986). Cover panels offer an economical alternative to featureless housing conditions with the potential to favorably impact welfare and productivity.

In addition to environmental features, stocking density, group size (GS), and pen size influence spatial and aggressive behavior (Keeling & Savenije 1995; Estevez et al. 1997; Charmichael et al. 1999; Nicol et al. 1999; Freed 2003). These factors, however, have not been tested independently of one another in published studies. Thus interpretations of behavioral effects must take into account confounding factors. For example, in order to examine the effects of stocking density while controlling GS, pen size must be manipulated. Any significant results cannot be uniquely attributed to stocking density alone, because pen size was concomitantly manipulated. Thus in this example stocking density and pen size are confounded with one another and their effects cannot be statistically distinguished from one another.

While acknowledging confounded effects, studies have demonstrated significant behavioral effects of group size (GS), pen size, and stocking density (Nicol 1987; Keeling 1994; Estevez et al. 1997 & 2003; Newberry & Hall 1997; Carmichael et al. 1999; Channing et al. 2001; Freed 2003). After increasing pen size by allowing outdoor access Estevez et al. (1997) found no difference in the amount of pen space used by individuals from different stocking densities. Channing et al. (2001) examined the effect of GS while holding stocking density constant and found that laying hens in all group sizes used a similar percentage of the available space. Similarly Newberry and Hall (1990) examined the effects of pen size and found an increased use of space as pen size and subsequently GS, were increased. Freed (2003) investigated the differences between stocking density and GS effects, and found that the amount of space available to a bird was the dominating factor for the use of space patterns in domestic fowl.

How animals distribute and use the space available to them is crucial to the welfare and productivity of domestic species maintained in captivity. Uniform, predictable environments such as commercial poultry houses offer domestic fowl little stimulation, decreasing welfare and ultimately productivity (Mench & van Tienhoven 1986; Wemelsfelder 1993; Wiepkema & Koolhass 1993; Mench 1998). This and future studies of effective, sensitive methods for determining use of space patterns are essential. Behavioral responses to environmental complexity (EC), and perhaps more importantly the detriment incurred in environments devoid of sufficient complexity, are important factors requiring additional investigation.

The techniques for measuring dispersal and the use of space in confined, domestic species are not fully developed. Confinement negates many of the assumptions that

underlie classical techniques developed for the study of wild species, namely freedom of movement and a bivariate normal distribution with increased use of center areas (White & Garrott 1990). We have chosen to generate core areas with a kernel density estimation technique adjusted for the confined condition of our test animals. This method is more sensitive than quadrant analysis, conveying additional information about how animals use the space available to them. Quadrant analysis has been used in similar studies (Cornetto & Estevez 2001b; Newberry & Shakelton 1997) and as the name implies involves dividing the available space into pieces, or quadrants, and comparing counts of the number of times animals appear in each quadrant. While this conveys information about the direct location of an animal it does not confer a detailed and specific value for the amount of space utilized, which is provided by core areas. Rather than quantifying the exact location of individuals, core areas detail the area of movement based on an animals recorded locations. In addition a visual plot of these location points and core areas can be generated to suggest preferences for specific locales within the available space. Core areas are calculated from the locations where an individual was recorded, similar to home range estimation techniques used with wild, radio-collared animals. From the total number of locations a distribution of core areas is created specifying the frequency or intensity of their use. These core areas convey the frequency, or probability, of detecting an animal within the given area.

The benefits of kernel density core area estimates are numerous. This technique produces consistent results (Worton 1995; Seaman & Powell 1996; Blundell et al. 2001). Because the core area captures the extent of movement by the animals, subsequent analyses from similar environmental conditions will reveal similar results. Quadrant

analysis however may not produce similar results because, while animals will most likely show similar extents of movement, they may not frequent the exact same locations between studies. Furthermore the results from quadrant analysis are dependent upon the choice of quadrant size. Kernel density estimation involved efficient mathematical techniques that are applicable across scientific fields, animal species, and units of measurements and can be used to estimate an animal's concentrated area of movement. This estimate for the extent of an animal's movement applies to both confined and free situations.

Minimum convex polygon is another technique used to quantify animal home ranges. The widest-reaching points over which the animal was located generate the polygon (Mohr 1947). While this technique conveys the minimum range over which a wild animal travels based on its observed movements, the specifics conveyed about confined environments are not particularly informative. Concerning confined domestic fowl, which cluster along pen walls (Newberry and Hall 1990; Cornetto et al. 2002), the polygon will be roughly equivalent to the pen size. Kernel density core areas, however, do not necessarily encompass all points and instead define the most important areas of activity for an animal. The information they convey, the extent to which the animal travels within the pen, is both representative and informative. The concept of core areas can be applied to other animals under similar environmental conditions. In addition to core areas, inter-bird distances, mainly in the form of nearest neighbor analyses (NN) are frequently used to determine social spacing behavior in domestic fowl (Banks 1984; Keeling and Duncan 1991; Keeling 1994; Keeling 1995).

This experiment investigated the effects of cover treatments and different group sizes on the spacing and aggressive behavior of young domestic fowl. We hypothesized that the level of environmental complexity (EC) would influence the spatial distribution patterns and aggressive strategies of domestic fowl. As EC increases birds should disperse and use larger pen areas when offered concealment and protection. We further expected these behavioral responses to follow basic behavioral ecology predictions, such that experimental GS would significantly impact the response to EC. Smaller group sizes, with increased susceptibility to predation, should have a greater response to EC than larger groups. Larger group sizes should foster diminished group cohesion, or inter-individual proximity, as group members move farther from one another and spread within the pen.

Methods and Materials

Facilities and Experimental Animals

This experiment was conducted at the University of Maryland's Upper Marlboro Applied Poultry Research Facility from March 17th 2003 through June 3rd 2003. A total of 336 one-day old male chicks were obtained from a commercial hatchery (Allen's Farm Inc., Salisbury DE). Upon arrival to the facility the chicks were randomly divided into eight groups of forty-two birds and were housed in separate pens. The pens were constructed of PVC piping and black netting, measuring 1.8m x 2.4m with a floor area of 4.5m^2 covered with 5cm of wood shavings. Birds were maintained on a 14L:10D lighting program in

an effort to promote slow growth and leg health. Temperature regulation followed commercial practices. Ventilation was provided by temperature controlled curtains and a central air tube and ceiling fans. In each pen, food was provided *ad libitum* through a central tubular hopper and water through a line of nipple drinkers (7 nipples p/pen, 6 birds per nipple) located along one side of the pen. The diet was specifically formulated to slow growth rate, consisting of 3 phases, starter (19% crude protein, 2800.00kcal/kg metabolizable energy), grower (17% crude protein, 2801.70 kcal/kg metabolizable energy), and finisher (19% crude protein, 3251.70 kcal/kg metabolizable energy). The starter phase was provided from days 0-14, the grower from 15-50, and the finisher from 50 until completion of the experiment at day 79. Mortalities were recorded daily.

Birds were tagged at three weeks of age on each side of the neck using the Swiftack for Poultry Identification System (Heartland Animal Health, Inc). Circular tags were made of sturdy laminated white paper, 5cm in diameter. Numbers were solid black and printed on both sides, ranging from 1 to 35. Seven birds per pen were left unmarked as replacements in the event of mortalities. For testing purposes each of the eight pens were divided in three experimental groups of 5 (GS_5), 10 (GS_{10}) and 20 birds (GS_{20}). Birds were permanent group members and for tested with the same individuals. Five individuals in each of the experimental GS per pen were designated, at random, as focal birds. If a tagged, non-focal bird died then a new individual was tagged with that same number. If a focal individual died we used the group member with the next highest tag number to complete the group for testing.

Experimental Design

For this study on the effects of GS and EC on the use of space and aggression in the domestic fowl we constructed three testing arenas, each measuring 2.25m x 7.25m with a floor area of 16.3m^2. We covered the floor with 5cm wood shavings and the walls in black plastic sheeting. Water was provided *ad libitum* from 14 nipple drinkers located in two lines at each end of the arena. Multiple arenas enabled each experimental GS from one home pen to be tested simultaneously. Each arena was marked with a grid system along sidewalls, as well as the long back wall opposite the main corridor. Sidewalls were marked with letters A-I, and the back wall was marked with numbers 1-29, all spaced 0.25m apart. This marking system created a readable grid of 261 0.25m^2 squares.

Each experimental GS was tested once under all three levels of EC – void, single, and quadruple (quad). The void treatment was a control and consisted of an empty arena, while the arenas for the single and quad treatments each contained panels constructed from white PVC pipe frames and a double-layer of screen mesh. All birds could be identified through the panel screens. The single treatment was comprised of a single panel, four meters long and 90 cm tall positioned in the center of the arena. The quad treatment was comprised of four panels, each one meter long and 90 cm tall staggered in a broken line such that panels did not overlap. The arena layout for each treatment is shown in Appendix 5-1.

For the test each of the experimental group sizes were caught by hand and transported in crates from one of the eight home pens to one of the testing arenas.

After all birds had been caught each crate was delivered to the center of an arena and all birds were released. Prior to testing all birds were habituated to the testing arena and transportation procedures during weeks one and two. During this habituation period each experimental GS was transported three times, once to each arena, and remained there for one hour. The order of testing was assigned at random and occurred between three and four weeks of age. Birds were transferred according to their respective GS, to one of the three arenas.

Measurements

Immediately following the transfer to the testing arena, and prior to the beginning of data collection, birds were given a 15-minute acclimation period. The initial part of testing lasted one hour and consisted of observational scan sampling. All arenas were observed at one-minute intervals, for one hour, and the location and identity of the five focal individuals were plotted on a scaled grid map along with the location of all remaining individuals. During the hour a total of twenty observational scans were collected for each of the three arenas. After the hour of use of space data collection each arena was observed separately for 15 minutes. During this time all aggressive interactions between birds were recorded together with the location within the arena where the interaction occurred. The ID of the birds involved as well as a designation of either 'giver' or 'receiver' of aggression was recorded. The order of observation was randomly assigned.

The scans were encoded by the Chickitizer v.4 software package (Sanchez and Estevez 1998). This software operates in conjunction with a digitizer (Advanced) to code each location in XY coordinates and append information such

as the pen and experimental GS as well as bird ID. From this data we were able to

calculate the core area estimates, at 30, 50 and 90% using the ArcView GIS (v

3.2) software and the Animal Movement Extension (v 2.04β; Hooge &

Eichenlaub 2000). Core area levels correspond to the probability of finding a bird

within the calculated area, and are constructed based on an assessment of

recorded positions. The output is an area measurement (m^2) that corresponds to

the amount of space over which an individual is suggested to traverse based on

the available data. We adjusted bandwidth of the kernel density estimator to 0.4.

This value was used since we determined from testing multiple reported [H]

values (Worton 1989; Seaman & Powell 1996; Blundell et al. 2001) that this

value produced the least amount of bias, given the pen size, while retaining the

most information. Two sets of core area measurements were calculated from the

location of focal individuals. First, a core area was determined for each individual

(Individual Core Area - ICA), and the second was calculated from the location of

all five focal birds taken together (Total Core Area - TCA). As opposed to a

traditional core area measurement TCA measures the amount of space used by all

five focal birds, essentially behaving like a measure of group dispersion. We have

assumed that the five focal individuals are randomly located within the entire

group. In addition to core areas, we computed inter-bird Euclidian distances such

as maximum and minimum distances between every pair of birds in each scan.

Maximum distance was defined as the farthest recorded distance and the

minimum distance was defined as the smallest recorded distance between any two

individuals. Nearest neighbor (NN) distances were also calculated from the

closest individual for each bird from each trial, averaged across all animals for each scan.

Inter-bird distances were separated into two components, expected distances based on random movement, and behavioral effects. In order to distinguish between the two we ran a simulation program (S-plus 6.1, MathSoft, Seattle, WA) based on the pen measurement and different GS. The results from this simulation for maximum, minimum and NN distances are shown in Appendix 5-2. The behavioral component for inter-bird distances was designated as the deviation from the random expectations, or observed values minus expected.

Statistical Analysis

All analyses were conducted using a Mixed Model ANOVA in SAS statistical analysis software (v. 8.1, SAS Institute, Cary, NC). Separate ANOVAs were conducted for each core are level, as well as for the minimum, maximum and NN distances and aggressive interactions. Model assumptions of normality and homogeneity of variance were tested. Square root transformations were performed on inter-bird distances and core area measurements to satisfy those assumptions. The experiment was designed as a factorial with experimental GS and EC levels analyzed as fixed factors. The model was adjusted for the covariance structure based on the fact that each GS was tested a total of three times and housed together. Because the covariance for GS being exposed to all treatment was estimated at zero for some measurements, it was removed from all analyses. All mean comparisons were reported using Tukey's LSD for Type 1 error rates (for review see Jones 1984).

Results

Individual Core Areas (ICA)

The 30% ICA was not significantly affected by GS ($F_{2,56}=2.86$, p=0.0659) nor by the different cover panel treatments ($F_{2,56}=0.52$, p=0.5987) or the interaction of GS and EC ($F_{4,56}=0.356$, p=0.8457). Similarly the 50% ICA (GS: $F_{2,56}=2.02$, p=0.1418; EC: $F_{2,56}=0.91$, p=0.4086; Interaction: $F_{4,56}=0.58$, p=0.6755) and the 90% ICA (GS: $F_{2,56}=0.64$, p=0.5294; EC: $F_{2,56}=0.95$, p=0.3943; Interaction: $F_{2,56}=1.52$, p=0.2083) were not affected by any of the experimental factors.

Total Core Areas (TCA)

Total core area was measured as the core area of five focal individuals and acted as an estimate of group dispersal. As GS increased, the five focal individuals should become more distant from one another, thus increasing the TCA calculation. The 30% TCA (Fig. 2-1a) was not significantly affected by EC ($F_{2,56}=0.51$, p=0.6026) nor the interaction ($F_{4,56}=0.58$, p=0.6774), but was significantly affected by GS ($F_{2,56}=10.44$, p <0.001). Likewise, the 50% TCA (Fig. 2-1b) was only affected by GS ($F_{2,56}=15.37$, p <0.0001) and not by EC ($F_{2,56}=0.17$, p=0.8466) or the interaction ($F_{2,56}=0.13$, p=0.9722). Similar results were obtained for the 90% TCA (Fig. 2-1c), as GS produced the only significant effect ($F_{2,56}=19.30$, p <0.0001). Both EC ($F_{2,56}=0.35$, p=0.7033) and its interaction with GS were not significant ($F_{4,56}=1.18$, p=0.3292).
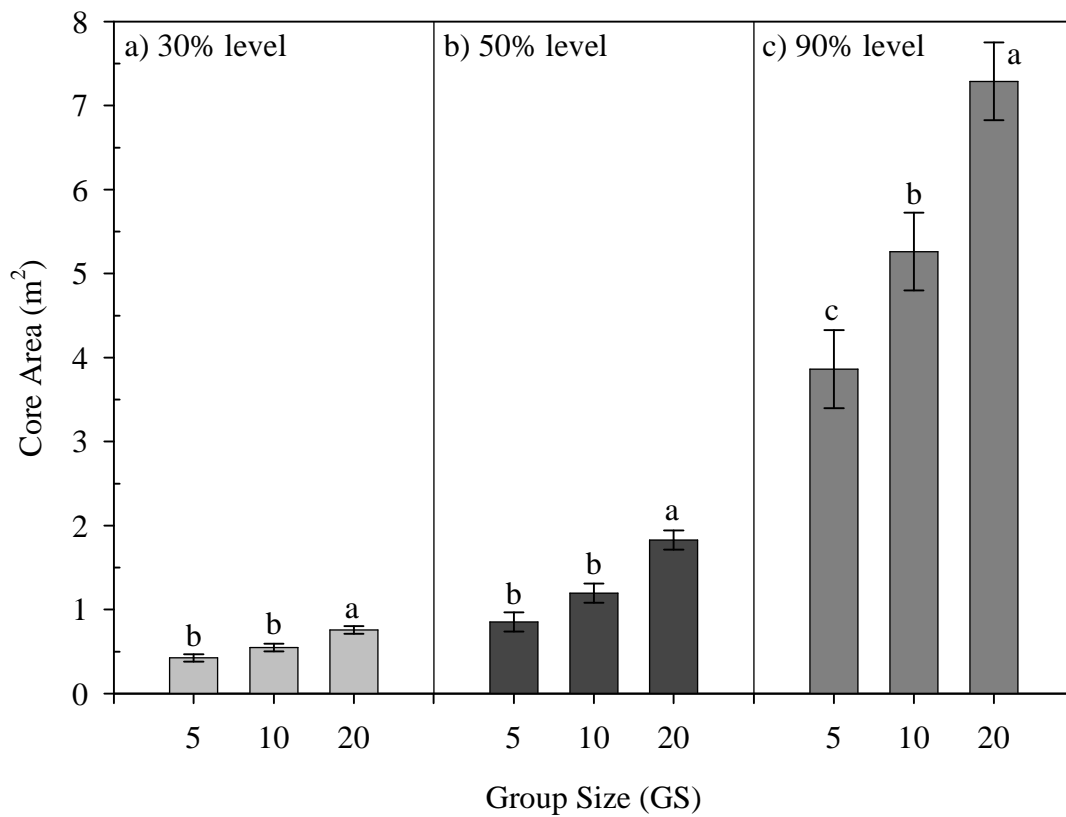
Figure 2-1. Total core area (TCA) calculated from all focal individuals at GS_5, GS_{10} and GS_{20}, for the 30% (a), 50% (b) and 90% (c) levels. Bars represent least squares means ($\pm$ SEM). Bars sharing any identical letters are not significantly different, $p > 0.05$; Tukey's adjustment.
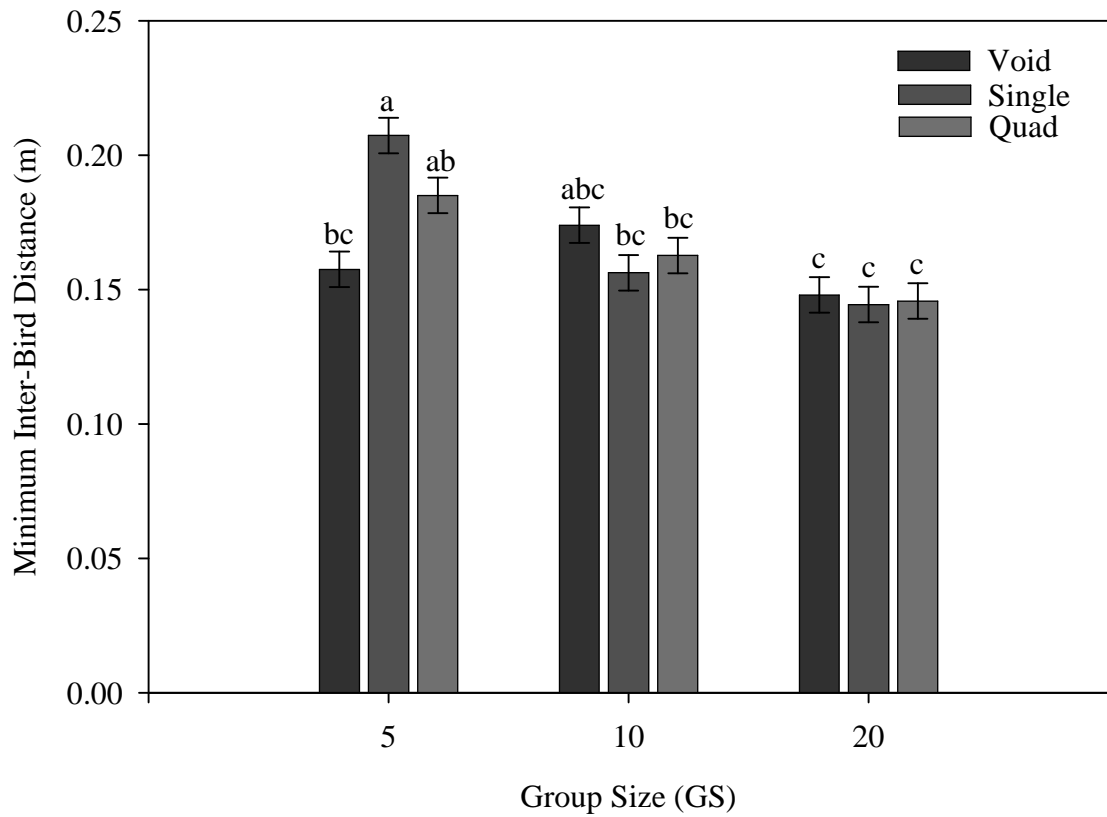
Figure 2-2. Minimum inter-bird distances for GS_5, GS_{10} and GS_{20}, and level of environmental complexity (EC). Bars represent least squares means ($\pm$ SEM). Bars sharing any identical letters are not significantly different, $p > 0.05$; Tukey's adjustment.

Inter-Bird Distances

When considering the minimum distance between any two birds in an experimental GS, under each EC (Fig. 2-2), the interaction of the level of EC and GS was significant ($F_{4,56}= 6.57$, p=0.0002). Because of the overwhelming effect of group size ($F_{2,56}=21.49$, p<0.0001) we have included this result in our discussion. EC was not significant ($F_{2,56}=1.26$, p=0.2927). The deviation from random for the minimum inter-bird distance was also significantly affected by the interaction of GS and EC ($F_{4,56}=6.94$, p=0.0001; Fig. 2-3). Again, because the F value was smaller than that for GS we have also discussed that main effect. GS was highly significant ($F_{2,56}=4256.39$, p<0.0001) but EC was not for the minimum inter-bird distance deviation from random ($F_{2,56}=1.48$, p=0.2359).

The maximum distance between any two birds was also significantly effected by GS ($F_{2,56}=151.34$, p<0.0001; Fig 2-4) but not by EC ($F_{2,56}= 0.75$, p=0.4749) or the interaction of the two ($F_{4,56}=0.12$, p=0.9736). The deviation from random for the maximum inter-bird distance was also affected by GS ($F_{2,56}=25.37$, p<0.0001; Fig 2-5) and not by EC ($F_{2,56}=0.56$, p=0.5762) or the interaction ($F_{4,56}=0.08$, p=0.9985).

The average NN distance considering all birds was affected by GS ($F_{2,56}=4.58$, p=0.0144) but not by EC ($F_{2,56}=0.15$, p=0.86308). The interaction of GS and EC was also significant ($F_{4,56}=4.35$, p=0.0039; Fig. 2-6). The deviation from random for the NN distance was also significantly affected by GS ($F_{2,56}= 2264.71$, p<0.0001) more so than the interaction of GS and EC ($F_{4,56}=4.73$, p=0.0023; Fig 2-7).
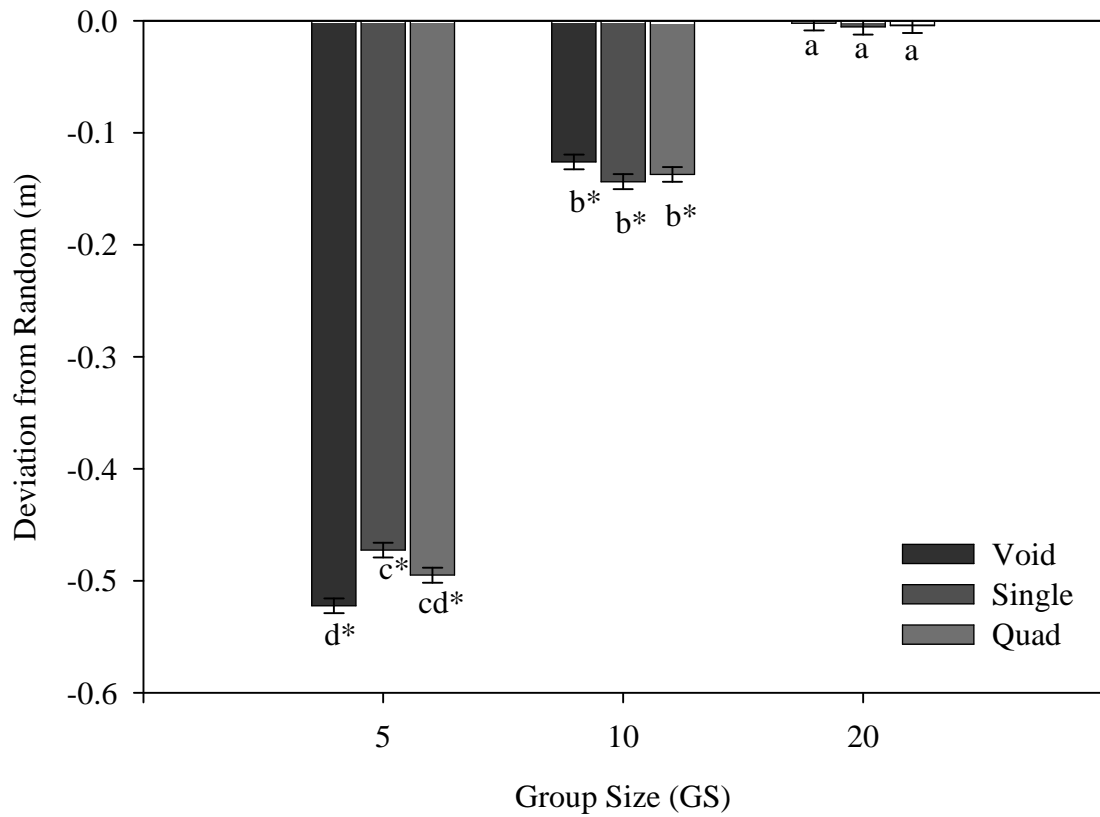
Figure 2-3. Minimum inter-bird distance deviation from random by group size (GS) and level of environmental complexity (EC). Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment. Bars designated with an asterisk (*) differ significantly from zero.
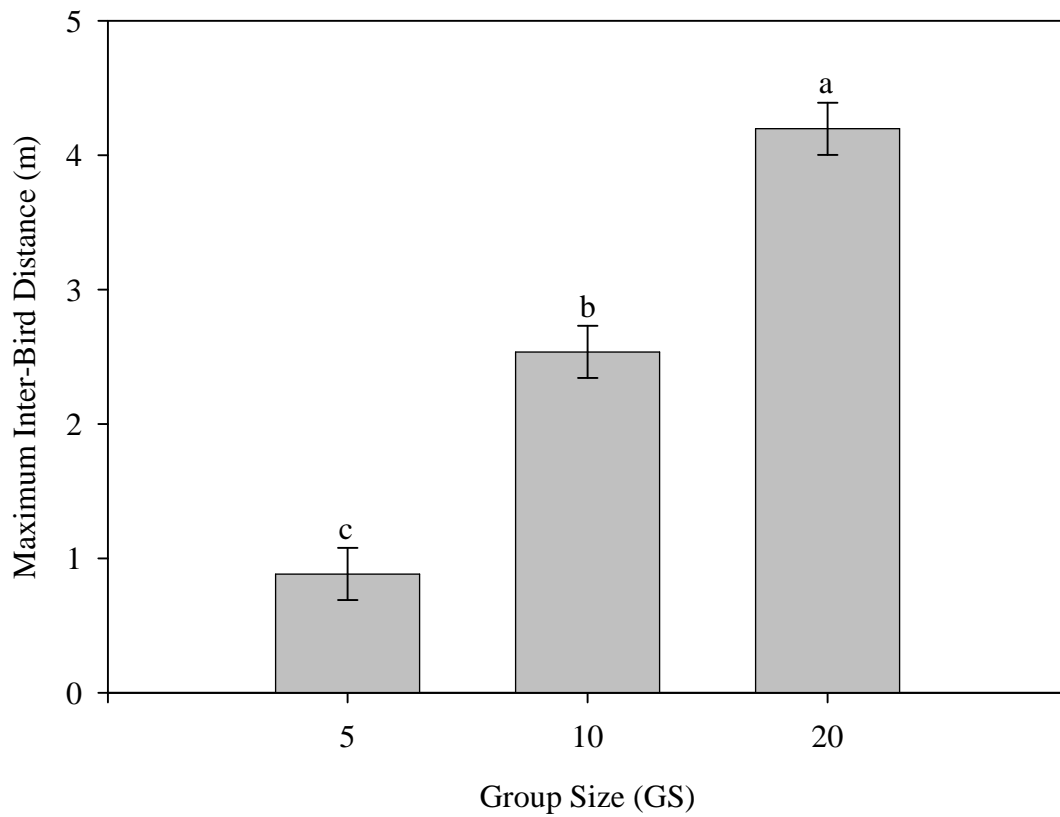
Figure 2-4. Maximum inter-bird distances by GS_5, GS_{10} and GS_{20}. Bars represent least squares means(± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.
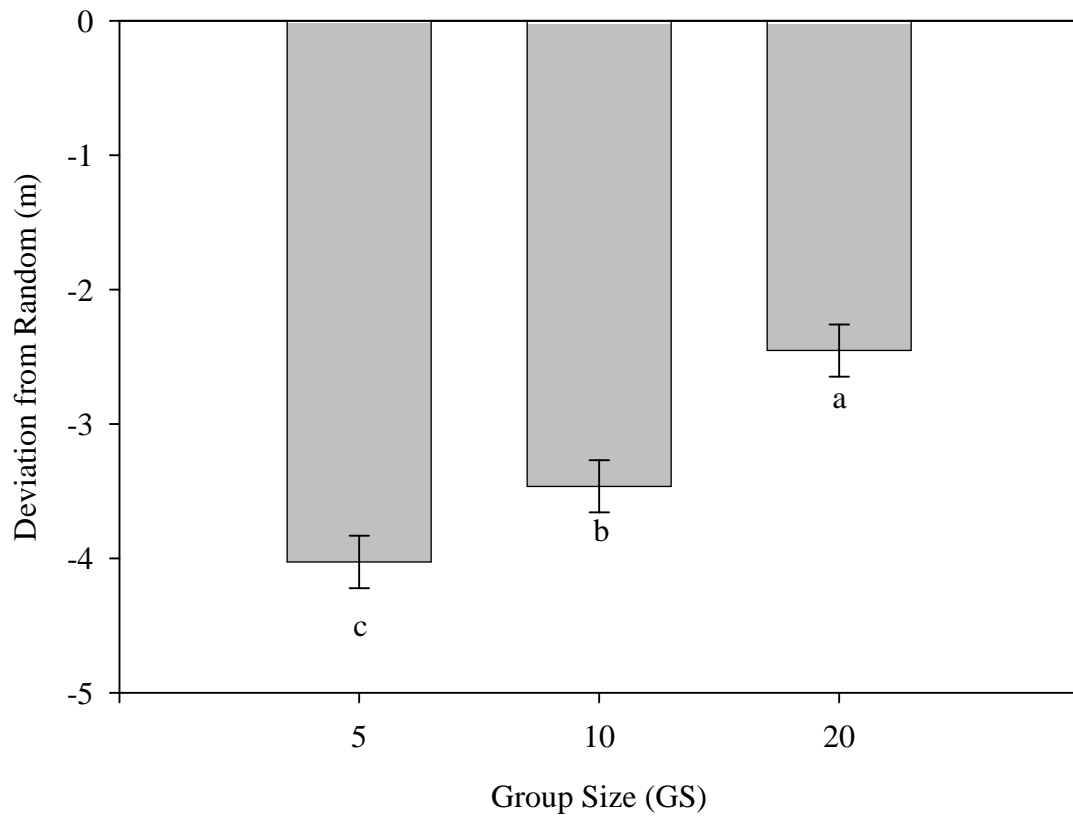
Figure 2-5. Maximum inter-bird distance deviation from random by group size (GS). Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment. All bars differ significantly from zero.
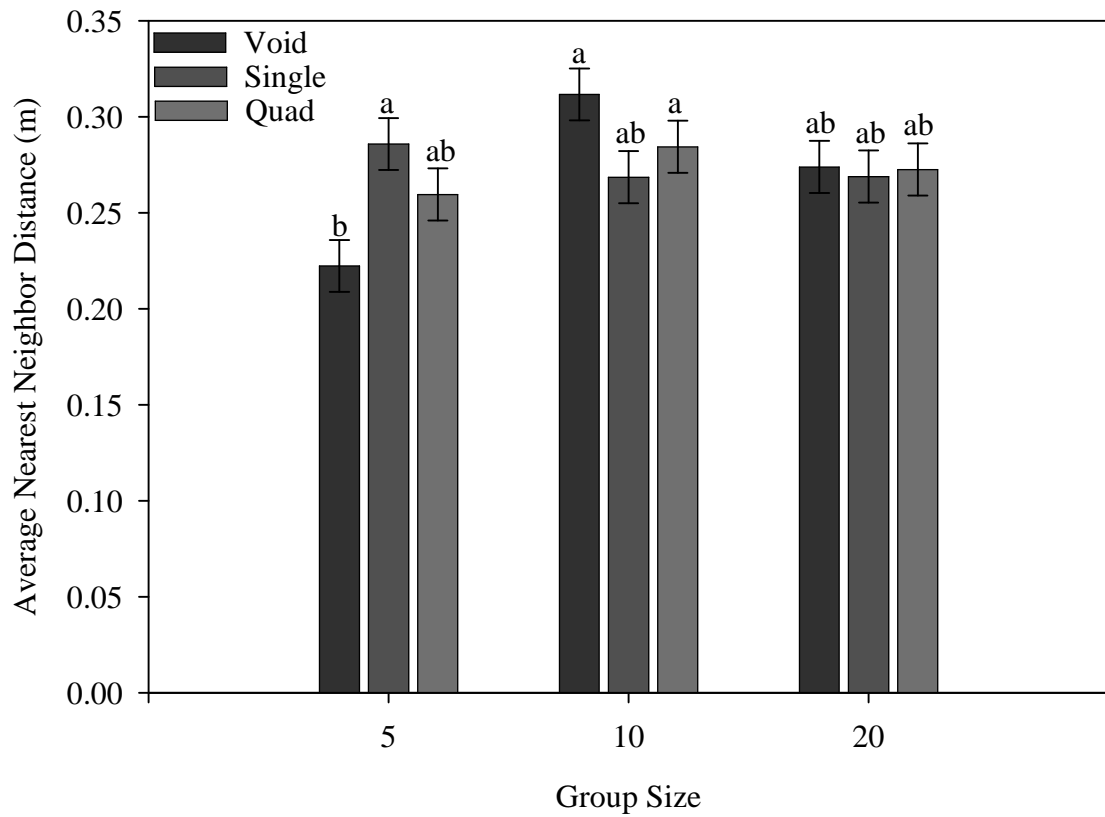
Figure 2-6. Nearest neighbor (NN) distance for GS_5, GS_{10} and GS_{20}, according to level of environmental complexity. Bars represent least squares means ($\pm$ SEM). Bars sharing any identical letters are not significantly different, $p > 0.05$; Tukey's adjustment.
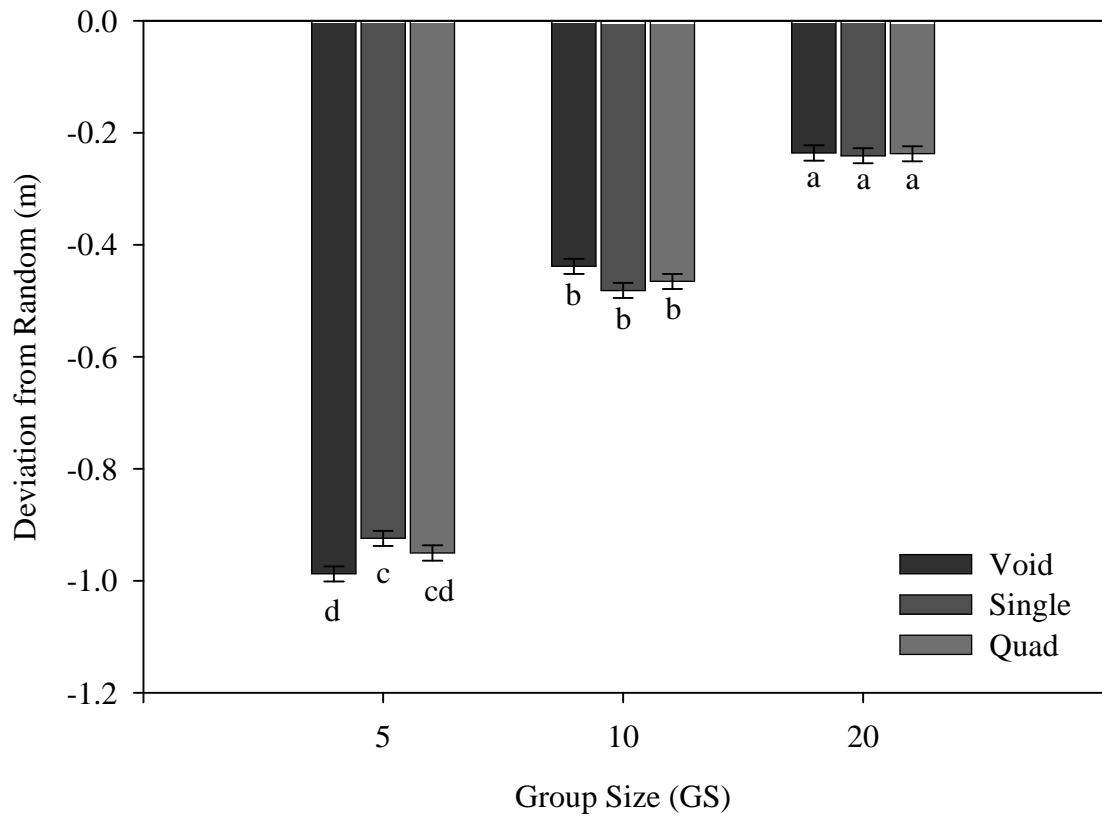
Figure 2-7. The deviation from random for the nearest neighbor (NN) distances, according to group size and level of environmental complexity (EC). Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment. All bars differ significantly from zero.

EC did not significantly affect the deviation from random for the NN distances ($F_{2,56}$=0.35, p=0.7061).

Aggression

There was no significant affect of either GS ($F_{2,54}$=0.57, p=0.5716) or EC ($F_{2,54}$=0.55, p=0.5774) on aggressive interactions. The order in which pens were observed determined the amount of time animals spent in the testing arena; this time effect was significant ($F_{2,54}$ = 4.58, p=0.0146). In the first observation we observed 0.81 ± 0.128 (mean ± SE) interactions per bird per minute, which was significantly more than the last observation with 0.37 ± 0.133 interactions (t=3.03, p=0.0104) however the first observation did not differ significantly from the second observation which had 0.65 ± 0.134 aggressive interactions (t=1.37, p=0.3612). Similarly the second observation did not differ from the third (t=1.53, p=0.2855). The only interaction effect of significance was for EC by GS ($F_{4,54}$=2.62, p=0.0451; Fig. 2-8), however no means were significantly different from one another.

Figure 2-8. Total number of aggressive interactions on a per bird basis for each 15-minute trial. Means ± SEM are separated by GS_5, GS_{10} and GS_{20}, according to level of environmental complexity. No means were significantly different, $p > 0.05$; Tukey's adjustment.

Discussion

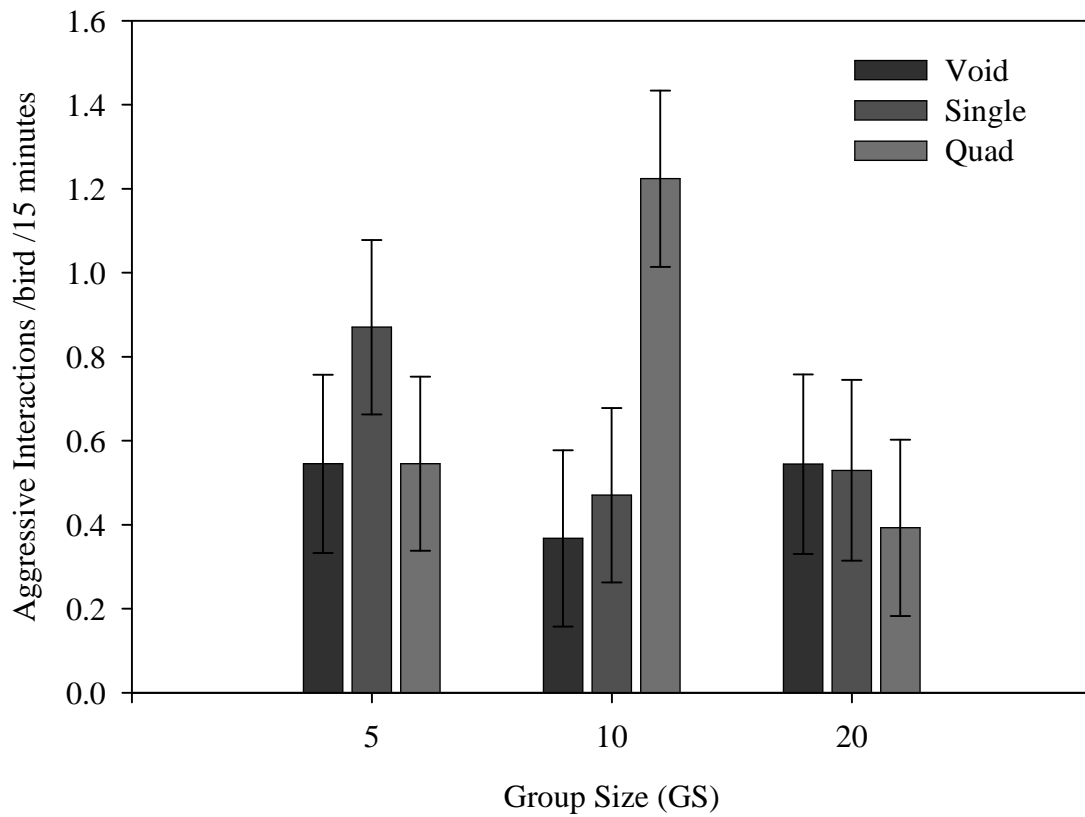Our results agree with others studies that have examined the influence of various environmental factors on the use of available pen space by domestic fowl. The behavioral effects of social factors such as stocking density and GS (Banks 1984; Keeling & Duncan 1991; Keeling 1994; Carmichael et al. 1999), physical factors such as pen size and physical features (Hughes 1980; Newberry & Hall 1990; Newberry & Shackleton 1997) and environmental conditions such as the provision of cover and perches (Keeling & Savenije 1995; Newberry & Shackleton 1997; Cornetto & Estevez 2002a; Cornetto & Estevez 2002b; Cornetto et al. 2003) have all been widely reported. The various environmental conditions in this study not only altered the total area utilized by the flock as a collective but also specifically affected inter-bird distances which were all significantly different than random. While TCA and maximum inter-bird distances increased with GS the minimum inter-bird and NN distances revealed complex changes in animal spacing according to the level of EC. Inter-bird distances were significantly smaller than random suggesting that each clumped to a greater degree than expected, but this clumping behavior was most pronounced in GS_5, with the greatest deviation.

The ICA levels were not significantly affected by GS, or EC. This suggests that despite different environmental conditions the extent of pen use was similar for all individuals. The most substantial factor influencing the extent of pen use appeared to be pen size, as it was constant across all group sizes and panel treatments. This finding is consistent with other studies, which have examined social and physical factors that may affect, or limit, pen use in domestic fowl (Newberry and Hall 1990; Channing et al. 2001). However our approach employed core area analysis as opposed to distance

traveled, minimum convex polygon or quadrant analysis, similar to the study of Estevez et al. 1997.

While experimental group sizes were housed together in a home pen, each expressed pronounced behavioral responses not only to the physical environmental changes but also to the changes in GS. The three experimental GS were housed together in order to control the background environment for each group, and to enable us to capture the immediate behavioral response of animals both to varying levels of EC and changes in GS. Concerning TCA, minimum, maximum and NN distances as well as aggression, behavioral responses were affected by GS despite similar background environmental conditions. We conclude that domestic fowl possess the capacity to immediately adapt to changes in environment and group size.

For the TCA, calculated from the simultaneous location of all focal birds, animals in larger groups consistently spread over a greater amount of the available pen space. If birds oblige a constant amount of individual space, then the total space occupied by 20 individuals should be greater than that of 5. A random, even distribution of birds should result in a larger TCA calculated for the 5 focal individuals in GS_{20}, followed by GS_{10} and lastly GS_5. While the amount of area occupied by the focal birds increased with GS, birds were not distributing themselves in order to maintain a constant amount of individual space, nor were they moving in random patterns with respect to inter-bird distances.

GS_5 and GS_{10} minimum distance deviations from random were all significantly smaller that zero, suggesting that birds within these two GS or maintained closer distances to one another than expected. GS_{20} minimum inter-bird distance deviations

were not significantly different from zero. This larger GS behaved more similarly to random and minimum distance was not affected by EC. Considering the minimum inter-bird distance EC had a substantial effect on GS_5, but this effect diminished with increasing GS and was in fact not evident for GS_{10} or GS_{20}. Only birds in GS_5 altered the distance of the closest neighbor according to the level of EC, with the closest neighbors in the void treatment. We expected these results from minimum distances and their deviation from random, in accordance with behavioral ecology and the anti-predatory function of flocking. The environment should exert greater influence on the behavior of smaller groups as compared to larger ones. Over short time periods larger group sizes may benefit most significantly from the protection of group size as opposed to the provision of panels, as seen by the lack of EC affects. Groups were only observed for one hour, and the immediate response to environmental changes was most dominated by physical environmental factors for GS_5 as compared to social factors for GS_{10} and GS_{20}.

The average NN distances followed a similar pattern to the minimum inter-bird distances. EC did not affect GS_{20} and GS_{10} individual's NN distances, or their deviation from random, however GS_5 was significantly affected by EC. Group cohesion was a measure of the average distance between individuals, or how close birds flocked together in relation to the random expectations. Overall GS_5 had the greatest group cohesion, with the smallest NN distances and the greatest deviation from randomness, particularly when in the void treatment. Group cohesion for individuals in GS_{10} and GS_{20} was not affected by the panel treatments.

TCA and NN distances supported our expectation that smaller GS would display a greater degree of flock cohesion, however this depends on the level of EC. Predation risk

decreases with increasing group size (Lima 1995). From an evolutionary perspective, birds are expected to maintain a more cohesive, or tightly knit group, at smaller GS (Caraco 1981; Carbone et al. 2003). If predation is the major force driving flock cohesion then individuals from smaller groups should stay closer to one another than birds in larger groups. Accordingly, animals from GS_5 maintained the smallest maximum inter-bird neighbor distances when compared to the two larger GS, and for all inter-bird distances were more deviant from random than the two larger GS.

Clark and Mangel (1984) predicted different patterns of group cohesion depending upon the motivations for group formation. If flock formation is predominantly a response to predation pressure, then groups should be large and highly cohesive. However if groups form in response to foraging strategies then groups should be smaller, and less cohesive in order to reduce competition and allow for independent searches. Keeling (1995) found that chickens maintained the greatest distance between themselves and flock mates while foraging. The author suggested that birds moved farther apart from one another so as to avoid foraging in areas that had previously been harvested by others. Similarly, Carbone et al. (2003) found that geese from larger flocks were more widely dispersed than geese from smaller flocks, and that larger flocks expanded at a faster rate. The authors hypothesized that this expansion of larger flocks was a product of the trade-off between predation risk and competition. Larger flocks provide better anti-predator protection than smaller ones, thus allowing individuals to relax flock cohesion. However with an increase in the number of foraging individuals comes greater competition between flock members. We found evidence of increasing flock dispersal with increasing GS, as NN distances were larger for GS_{10} and GS_{20} than GS_5. Furthermore, the deviation

from randomness was greatest for GS_5. This deviation decreased as GS increased, suggesting stronger behavioral affects on inter-bird distances at small GS as compared to larger ones.

The proximity of a neighbor is not as significant on predation as group dispersal. It is likely that a threshold limit for cohesion, or close distance to conspecifics exists, after which no additional protection is gained from flocking. This threshold is directly related to GS, increasing as flock size increases. While individuals need to be close enough to one another to both detect and transmit information about predators, after this threshold of inter-individual proximity is satisfied closer individuals offer no additional advantages. Maximum inter-bird distances measure the amount of space individuals in a group are willing to place between themselves; this distance has a direct impact on predation (Carbone et al. 2003). As GS increased the greatest distance between any two individuals also increased, as the overall area occupied by the birds was greater. The TCA, in conjunction with NN distances, suggested that individuals increased pen usage with increasing GS. The effects of EC on inter-bird distances differed across GS. Interactions in minimum and NN distances, and their deviation from random, illustrated that GS_5 was more susceptible to the effects of EC than GS_{10} or GS_{20}.

Overall there was a low level of aggression, regarding aggressive interactions,. While there was a significant interaction of EC and GS, no means differed significantly from one another; the most significant result was that the groups responded differently to the various levels of EC. The amount of aggression seen was most significantly impacted by time difference between the first and last arena to be observed. There was a linear decline in aggression as the length of time in the test arena increased. The first and last

observations showed the greatest and least number of aggressive interactions, respectively. Prior to the onset of the observational period for aggressive interactions individuals were in the arena for one hour, during which spatial sampling occurred. At the end of testing the third and final GS to be observed had been in the testing arena for an hour and 45 minutes while the first to be observed only remained in the arena for an hour and 15 minutes. This additional time leads to the difference in number of aggressive interactions observed. We suspect that the transportation process and subsequent acclimation to the testing arena had an overwhelming effect on aggression, blocking the effects of environmental conditions such as GS or EC. Domestic fowl naturally form social hierarchies in small group sizes (Rushen 1982; Banks et al., 1979; Mankovich & Banks, 1982; Banks, 1984) and utilize aggressive threats and pecks maintain these hierarchies (Banks 1984; Banks et al. 1979; Stahl et al. 2001). Other studies have noted differential effects of GS on aggressive behavior, namely a curvilinear relationship. At small group sizes aggression increased with GS (Al-Rawi & Craig 1975; Hughes & Woodgush 1977) but once GS grows larger, aggression begins to decrease (Estevez et al. 1997; Freed 2003). Because aggression was significantly impacted by the order of observation, we speculated that activity levels most likely dropped throughout the duration of the trial, leading to fewer aggressive interactions in the last arena to be observed as compared to the first. When Newberry (1999) provided chicken the opportunity to explore a novel area birds initially rushed into the new space. However after the first 5 minutes the number of birds crossing over the threshold decreased. A similar burst of activity may have occurred in this study.

This experiment differed from previous experiments involving cover panels (Newberry & Hall 1997; Cornetto & Estevez 2001a,b; Cornetto et al. 2002) in that birds were transferred to an experimental arena during which time they encountered cover panels that altered the level of EC. While we found the most significant results of EC at smaller group sizes, previous studies have also shown a substantial effect at much larger group sizes. Our experimental protocol may have affected behavior of the fowl in a way that altered otherwise prevailing reactions to the provision of cover and differences in EC. GS_{20} may require a greater amount of time to become acclimated to panels and fully explore their benefits. In smaller group sizes there could be stronger pressure to seek protection and cover, whereas large group size affords individuals this protection. Learning may be an important factor shaping the use of panels in larger group sizes, which lack this strong pressure to seek cover and protection, as other studies have found panels to have a significant impact (Cornetto & Estevez 2001a,b). Our results confirm the importance of GS and social environments on use of space. Smaller group sizes were more significantly affected by EC than larger group sizes. GS_{20} individuals were the least affected by the level of EC, and GS_{10} individuals demonstrated the widest inter-bird distances greatest group spread.

Chapter 3: Influence of Patch Locations Mediated by Group Size on Aggression and Use of Space

Abstract

Use of space and aggressive interactions in the domestic fowl (*Gallus gallus domesticus)* were investigated under various group sizes, patch locations and levels of patch accessibility. Birds were tested in three experimental group sizes of five, 10, and 20 individuals per group and three patch location arrangements. This experiment consisted of two phases; during phase one groups had free access to all patches but in phase two patch access was restricted to a single individual. Groups were moved to a testing arena containing a single large patch, two medium-sized patches or four small patches. In all situations the total amount of food resources was identical. Individual and total core areas, as well as maximum, minimum, and nearest neighbor inter-individual distances were affected by group size, patch location, and patch accessibility. Birds in different experimental group sizes responded differently to patch locations. The minimum inter-individual distances for groups of five birds were affected by patch location while groups of 10 and 20 individuals were not. As expected maximum inter-bird distances and total core areas increased with GS. Aggression increased with group size only when patch access was restricted. Because the three experimental group sizes were temporarily created from a larger home group housed together, the results of this experiment demonstrate the capability of domestic fowl to immediately adapt their use of space and inter-individual distances according

to environmental conditions, and responded in ways that are consistent with the

predictions of optimal foraging theory.

Introduction

The dispersal and availability of resources within an animal's environment has a significant impact not only on the specific use of those resources, but also on the use of space (Mench & van Tienhoven 1986; Grigor et al 1995b; Arcis & Desor 2003), and on group dynamics for flocking species (Clark & Mangel 1984; Grant 1993; Caraco et al. 1989). The costs and benefits associated with group size shape individuals' flocking and foraging strategies (Clark & Mangel 1984). Resource patchiness is important as individuals attempt to optimize the costs and benefits associated with competing behavioral strategies. Individuals gain enhanced predator avoidance by flocking. However in group foraging, competition between individuals increases with increasing group size (Clark & Mangel 1984). Patterns of resource distirbution heavily impact an animal's ability to defend resources (Carpenter 1987; Grant 1993). Dominance hierarchies and social status are critical in determining an animal's access to, and share of, resources (King 1965; Banks 1984; Caraco et al. 1989; Keeling 1995; Pagel & Dawkins 1997; Stahl et al. 2001; Dubois et al. 2003).

Foraging strategies are influenced by the same environmental factors that impact survival and fitness. Optimality is achieved by minimizing the amount of energy expended gaining access to a resource, for example - search time, handing time and fighting, and by maximizing the energy gained from those resources. While the factors influencing the foraging strategies of wild animals are well documented, such as patch and nutrient quality (Lewis 1980; Alonso et al. 1995; Morris et al. 2002) or social dominance (Sullivan 1984; Caraco et al. 1989; Carrascal & Moreno

1992), the behavior of domestic species, maintained under unnatural, confined environmental conditions, has been less thoroughly investigated.

Marginal value theory (Charnov 1976; Parker & Stuart 1976) predicts that animals exploit patches based upon both their relative quality and also their distance from one another. Concerning group foraging species, patches present a situation in which multiple individuals may monopolize access. At small group sizes and with a single small resource, dominant individuals attempt to monopolize access while subordinates are relegated to waiting (Banks et al. 1979; Banks 1984; Pagel & Dawkins 1997). However as the resource patch grows in size it becomes more difficult for a single individual to defend and animals should switch from resource defense to tolerance, or sharing (Brown 1964). At this point the benefits gained from monopolization do not justify the costs of defense, which include risk of injury, energy expenditure and loss of feeding opportunities while engaged in defensive behaviors. With numerous close patches it is possible for multiple individuals to gain access, as patch defense by a single individual would be too costly. The decisions of group foragers must be based not only on social position, but relative costs and benefits of defense that are directly related to the distribution of resource patches.

Although genetic selection has successfully improved the performance of domestic animals their behavioral patterns have been altered as a consequence of this selection (Mench 1988; Jones & Hocking 1999; Andersson et al. 2001; Schutz & Jensen 2001; Schutz et al. 2001). Therefore their foraging strategies may not be appropriate in current housing environments. We would expect that because of the absence of natural selection to act upon and shape bird behavior and foraging

strategies that their response to unfamiliar group sizes and patches may be contrary to the predicted optimal foraging strategies. Done et al. (1996) found that domestic pigs oriented themselves according to trough size, rather than the specific amount of food poured into the trough. Furthermore, once the food was poured pigs did not switch to a trough with more food immediately, but rather reacted only to diminished returns at their chosen trough. Non-optimal decisions may lead to an increase in stress, aggression and other behavioral changes (Done et al.1996), which have been shown to diminish weight gain and productivity as well as overall well-being (King 1965; Gvaryahu et al. 1994; Estevez et al. 1997; Hughes et al.1997; Mench & Morrow-Tesch 1998). Dispersing resources to beneficially manipulate behavioral strategies can maximize both animal welfare and productivity.

The manner in which domestic species use the available space is an important issue to both animal production and welfare. Movement patterns may depend not only on the presence of conspecifics (Freed 2003), but also on the location of resources (Estevez et al. 2002; Arcis & Desor 2003). Previous experiments incorporating enrichment, such as perches or cover panels, have found significant impacts on spacing and movement patterns (Newberry & Shackelton 1997; Channing et al. 2001; Cornetto & Estevez 2001b). These elements increased environmental complexity, which is lacking in uniform litter-floor production houses. Research has also shown that group size (GS) and group dynamics, stocking density, and pen size all have important consequences on how animals move and use space in confined environments (Banks et al. 1979; Newberry & Hall 1990; Keeling 1994; Estevez et al. 1997; Carmichael et al.1999; Freed 2003).

In this experiment we examined how variations on environmental parameters affect the foraging strategies and use of space in the domestic fowl. The broiler chicken strain used for this experiment has been bred for generations via intense artificial selection for high growth rate and performance and is typically reared in unnaturally large groups with homogeneously distributed non-depleting resources. Conditions in production environments contradict wild conditions, namely small GS and heterogeneously clumped, non-abundant food resources. Unlike confined domesticated species, wild animals rarely encounter food abundance such that resource defense becomes more costly than a scramble foraging strategy (Grant 1993). Despite artificial selection pressures and unnatural environments, we hypothesized that domestic fowl are capable of adapting their foraging and behavioral strategies according to changes in their environments, both social and physical. We predicted that birds would immediately adjust their behavior to a new environment differing not only in the type and dispersal of resources but also in the number of conspecifics present. Our particular experimental protocol allowed us to measure the immediate behavioral repercussions of new GS as well as new environmental conditions while controlling for background social experiences.

Methods and Materials

Facilities and Experimental Animals

This experiment was conducted at the University of Maryland's Upper Marlboro Applied Poultry Research Facility from March 17th 2003 through June 3rd 2003. A total of 336 one-day old male chicks were obtained from a

commercial hatchery (Allen's Farm Inc., Salisbury DE). Upon arrival to the facility the chicks were randomly divided into eight groups of forty-two birds and were housed in separate pens. The pens were constructed of PVC piping and black netting, measuring 1.8m x 2.4m with a floor area of 4.5m^2 covered with 5cm of wood shavings. Birds were maintained on a 14L:10D lighting program in an effort to promote slow growth and leg health. Temperature regulation followed commercial practices. Ventilation was provided by temperature controlled curtains and a central air tube and ceiling fans. In each pen, food was provided *ad libitum* through a central tubular hopper and water through a line of nipple drinkers (7 nipples p/pen, 6 birds per nipple) located along one side of the pen. The diet was specifically formulated to slow growth rate, consisting of 3 phases, starter (19% crude protein, 2800.00kcal/kg metabolizable energy), grower (17% crude protein, 2801.70 kcal/kg metabolizable energy), and finisher (19% crude protein, 3251.70 kcal/kg metabolizable energy). The starter phase was provided from days 0-14, the grower from 15-50, and the finisher from 50 until completion of the experiment at day 79. Mortalities were recorded daily.

All birds were tagged at three weeks of age on each side of the neck using the Swiftack for Poultry Identification System (Heartland Animal Health, Inc). Circular tags were made of sturdy laminated white paper, 5cm in diameter. Numbers were solid black and printed on both sides, ranging from 1 to 35. Seven birds per pen were left unmarked as replacements in the event of mortalities. For testing purposes each of the eight pens were divided in three

experimental groups of 5 (GS$_5$), 10 (GS$_{10}$) and 20 birds (GS$_{20}$). Five individuals in each of the experimental GS per pen were designated, at random, as focal birds. If a tagged, non-focal bird died then a new individual was tagged with that same number. If a focal individual died we used the group member with the next highest tag number to complete the group for testing.

Experimental Design

For this study we constructed three testing arenas, each measuring 2.25m x 7.25m with a floor area of 16.3m^2. We covered the floor with 5cm wood shavings and the walls in black plastic sheeting. Water was provided *ad libitum* from 14 nipple drinkers located in two lines at each end of the arena. Multiple arenas enabled each experimental GS from one home pen to be tested simultaneously. Each arena was marked with a grid system along sidewalls, as well as the long back wall opposite the main corridor. Sidewalls were marked with letters A-I, and the back wall was marked with numbers 1-29, all spaced 0.25m apart. This marking system created a readable grid of 261, 0.25m^2 squares.

For each test one experimental GS was transported in crates from one of the eight home pens to the testing arena. Habituation to the testing arena and transportation procedures occurred from one to two weeks of age, during which time all experimental group sizes from a single home pen were transported together three times, once to each arena, and remained there for one hour. Birds were habituated to the food at one week of age when it was

scattered in the home pen hoppers containing their normal feed. This was done for three consecutive days, after which the food was not presented again until testing.

Testing occurred between ages five and eight weeks of age. This experiment had two distinct phases, a free access phase and restricted access phase. In the first phase groups were given free access to resources while in the second access was limited to a single individual. Birds were between five and six weeks of age for the first part of testing, and seven to eight weeks of age during the second. GS were tested in random order. Birds were transferred according to their respective GS, to one of the three arenas. Birds were caught by hand in their home pen and were placed in crates with experimental group members. After all birds had been caught each crate was delivered to the center of an arena and all birds were released.

To simulate different patch treatments, food was arranged in three different arrangements that mimicked patchy resources and were labeled patchy, spread and clumped. Four brown plastic dishes, 8cm in diameter and 2cm in depth, were arranged on 12cm high platforms to create the different resource patches. The patchy treatment consisted of four small patches created by four elliptical platforms each holding one dish. Each patch was placed in the periphery of the arena, close to the corners of the testing arena, 0.75m from the sidewalls and 0.5m from the back and front walls. The spread treatment consisted of two elliptical platforms, each containing two dishes. These platforms were placed 1.25m from the center of the arena to create two

medium-sized patches. The clumped treatment consisted of one large elliptical platform placed in the center of the arena, holding all four dishes. The distribution patterns for each resource treatment are shown in Appendix 5-3. Each experimental group size was exposed to every patch location scenario.

During each trail a total of 10 grams of food, containing 44% crude protein, was available per bird. This total was then equally divided between the 4 dishes, such that for GS_5 each individual dish contained 12.5g of cat food, while for GS_{10} each dish contained 25g, and for GS_{20} each dish contained 50g of cat food. For the second phase the experimental design was identical but patch access was now restricted to only a single bird. This was achieved by completely lining each patch with transparent plastic laminate sheeting (0.23m x 0.37m) except for a 4 cm opening on one of the sides. Each experimental GS, from each home pen, was again tested under all three patch locations, patchy, spread and clumped.

Measurements

Immediately following the transfer to a testing arena, and prior to the beginning of data collection, birds were given a 15-minute acclimation period. Observations started after the acclimation period, at which point food was added to each patch. Three experimental group sizes were simultaneously tested during one hour. The initial part of testing lasted one hour and consisted of observational scan sampling. All arenas were observed at one-minute intervals, for one hour, and the location and identity of the five focal individuals was plotted on a scaled grid map along with the location of all

remaining individuals. During the hour a total of twenty observational scans were collected for each of the three arenas one for each one-minute interval.

Immediately following the sampling period each patch was weighed, and re-filled with the same amount of food in preparation for the aggression observational period. After the initial use of space data collection each arena was observed separately for 15 minutes at which time all aggressive interactions between birds were recorded. The order of observation was randomly assigned, allowing any effects of time spent in the arena to be discerned.

The scans were encoded by the Chickitizer v.4 software package (Sanchez and Estevez 1998). This software operates in conjunction with a digitizer (Advanced) to code each location in XY coordinates and append information such as the pen and experimental GS as well as bird ID. We then employed a non-parametric kernel density estimation method to calculate the core area estimates, at 30, 50 and 90% using the ArcView GIS (v 3.2) software and Animal Movement Extension (v 2.04β; Hooge & Eichenlaub 2000). Core area levels correspond to the probability of finding a bird within the calculated area, and are constructed based on an assessment of recorded positions. The output is a specific numerical area (m^2) that corresponds to the extent of area over which an individual is suggested to traverse based on the available data. We adjusted the bandwidth of the kernel density estimator to 0.4. This value was used since we determined from testing multiple reported [H] values (Worton 1989; Seaman & Powell 1996; Blundell et al. 2001) that

this value produced the least amount of bias, given the constrained possible area, while retaining the most information. Two sets of core area measurements were calculated from the location of focal individuals. First, a core area was determined for each individual (Individual Core Area - ICA), and the second was calculated from the location of all five focal birds taken together (Total Core Area - TCA). As opposed to a traditional core area measurement TCA measures the amount of space traversed and occupied by all five focal birds, essentially behaving like a group dispersion measurement. In addition to core areas, we computed inter-bird Euclidian distances such as maximum and minimum distances between any two birds in each trail. Maximum distance was defined as the farthest recorded distance and the minimum distance was defined as the smallest recorded distance between any two individuals. Nearest neighbor (NN) distances were also calculated from the closest individual for each bird from each trial, averaged across all animals for each scan.

Inter-bird distances were separated into two components, expected distances based on random movement, and behavioral effects. In order to distinguish between the two we ran a simulation program (S-plus 6.1, MathSoft, Seattle, WA) based on the pen measurement and different GS. The results from this simulation for maximum, minimum and NN distances are shown in Appendix 5-2. The behavioral component for inter-bird distances was designated as the deviation from the random expectations, or observed values minus expected.

Statistical Analysis

All analyses were conducted using a Mixed Model ANOVA in SAS statistical analysis software (v. 8.1, SAS Institute, Cary, NC). Separate ANOVAs were conducted for each core area level, as well as for the minimum, maximum and NN distances, aggression and patch consumption. Model assumptions of normality and homogeneity of variance were tested and adjustments were made as necessary. Aggression values were log transformed and core areas were square root transformed to better satisfy model assumptions. The experiment was designed as a factorial with experimental GS and patch location treatments analyzed as fixed factors. The model was adjusted for the covariance structure based on the fact that each GS was tested a total of three times, and that each pen held three separate group sizes. Because the covariance for group sizes being exposed to multiple patch locations was estimated at zero it was subsequently dropped from the model. All mean comparisons were reported after Tukey's LSD for Type 1 error rates (for review see Jones 1984).

Results

Free Access Phase

Individual Core Area (ICA)

The results indicate that the 30% ICA were not significantly affected by GS ($F_{2,53.4}= 0.38$, p= 0.6876), patch locations ($F_{2,53.4}= 2.82$, p= 0.0683) or the interaction of two factors ($F_{4,54}= 0.69$, p= 0.5996).

The 50% ICA however were significantly affected by patch locations ($F_{2, 53.3}$= 3.32, p= 0.0439; Fig. 3-1) but were not affected by GS ($F_{2,53.3}$= 1.06, p= 0.6871), or the interaction ($F_{4, 53.8}$= 0.57, p= 0.6871. Concerning the 90% ICA, GS ($F_{2, 52.9}$=2.11, p=0.1317) and the interaction of GS and patch locations ($F_{4, 53.5}$=0.19, p=0.9417) were not significant factors while the effect of patch locations alone bordered on significance ($F_{2, 52.9}$= 3.02, p= 0.0574).

Total Core Area (TCA)

The interaction of the two factors, group size and patch locations, was significant on the 30% estimation ($F_{4,53.9}$= 3.36, p= 0.0158; Fig. 3-2). The 50% TCA were only significantly affected by GS ($F_{2,53.3}$= 12.00, p< 0.0001; Fig. 3-3a) and were not affected by the patch locations ($F_{2,53.3}$= 0.10, p= 0.9036). The interaction of these two factors was also not significant ($F_{4,53.9}$= 2.51, p= 0.0527), but did indicate likely behavioral differences in reaction to the patch locations across GS. For the 90% TCA, as with the 50% TCA, only GS was significant ($F_{2,52.8}$= 28.35, p< 0.0001; patch locations: $F_{2,52.8}$= 1.89, p= 0.1606; interaction: $F_{4,53.3}$= 1.42, p=0.2414; Fig. 3b).
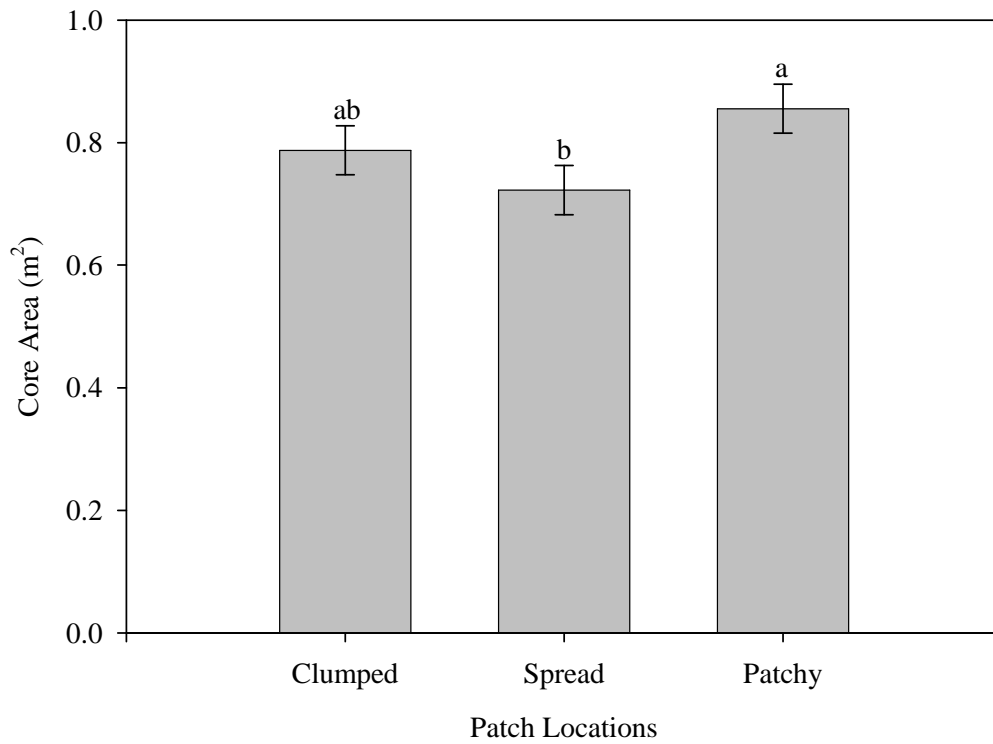
Figure 3-1. Individual core area (ICA) measurements at the 50% level for the free access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.
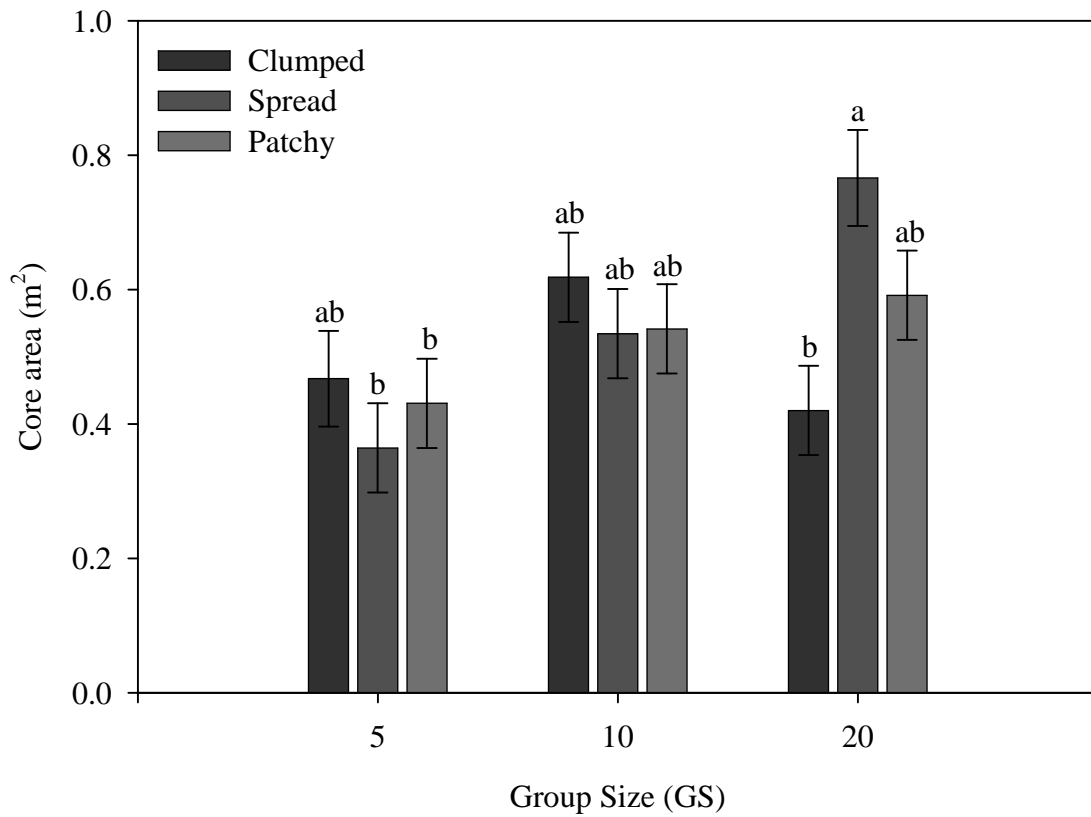
Figure 3-2. Total core area (TCA) measurements at 30%, according to the interaction of GS and patch locations for the free access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.
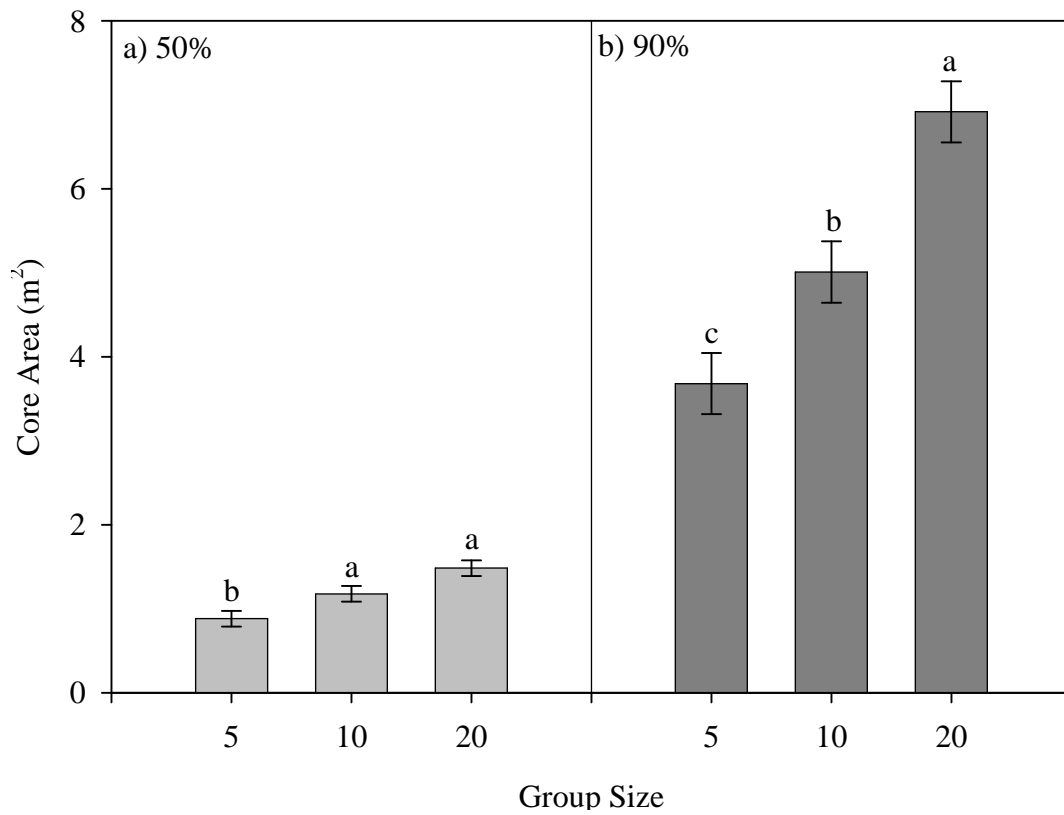
Figure 3-3. Free access phase total core area (TCA) measurements at 50% (a) and 90% (b) levels. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.

<u>Inter-Bird Distances</u>

The minimum inter-bird distance was significantly affected by the patch locations ($F_{2,52.4}$= 3.45, p=0.0390, Fig. 3-4a) as well as GS ($F_{2,52.4}$= 51.60, p< 0.0001, Fig. 3-4b) but not by the interaction of these two factors ($F_{4,53}$= 0.30, p=0.8796). Similarly the deviation from random for the minimum inter-bird distance was significantly affected by GS ($F_{2,52.5}$=2776.90, p<0.0001; Fig. 3-5) but not by patch locations ($F_{2,52.5}$=3.08, p=0.0544) or the interaction of the two ($F_{4,52.4}$=0.23, p=0.9183). The maximum distance between any two birds was affected by GS ($F_{2,51.5}$= 56.15, p< 0.0001) and the patch locations ($F_{2,51.5}$= 3.32, p=0.0441) as well an interaction ($F_{4,52.2}$= 4.73, p=0.0025; Fig. 3-6). Despite the interaction we discuss the strong effect of GS due to its much higher F value. There was a similar pattern of significance concerning the deviation from random for the maximum inter-bird distances. The interaction was significant ($F_{4,52.3}$=5.96, p=0.0005; Fig. 3-6), however the main effect of GS ($F_{2,51.6}$=15.25, p<0.0001) was more significant while the effect of patch locations on the deviation from random for the maximum inter-bird distance was not as significant ($F_{2,51.6}$=3.61, p=0.0342). NN distance was also significantly impacted by GS ($F_{2,51.7}$ = 3.82, p< 0.0284; Fig. 3-6), but not patch locations ($F_{2,51.7}$ = 0.46, p=0.6364) or the interaction of the two ($F_{4,52.5}$ = 0.48, p=0.7511). The deviation from random for the NN distance was also affected by GS

($F_{2,52}=141.98$, p<0.0001, Fig. 3-7) but not by patch locations ($F_{2,52}=0.24$, p=0.7864) or the interaction of the two ($F_{4,52.9}=0.34$, p=0.8481).

Patch Consumption

The percent of total patch consumption was not affected by the patch locations ($F_{2,49.2}=$ 0.10, p= 0.9090), GS ($F_{2,49.2}=$ 2.13, p= 0.1302), or the interaction of the two ($F_{4,50.4}=$ 0.92, p= 0.4599). On average birds consumed 78.7 ± 4.91% (mean ± SEM) of the available food.

Aggression

The frequency of aggressive interactions measured during the 15-minute observation period, was not affected by the patch locations ($F_{2,53.8}=$ 1.67, p= 0.1978), GS ($F_{2, 53.8}=$ 0.10, p= 0.9025), or the interaction of the two factors ($F_{4,43.5}=$ 1.19, p= 0.1858). The effect of observational order was also not significant ($F_{2, 53.8}=$ 2.21, p=0.1192).
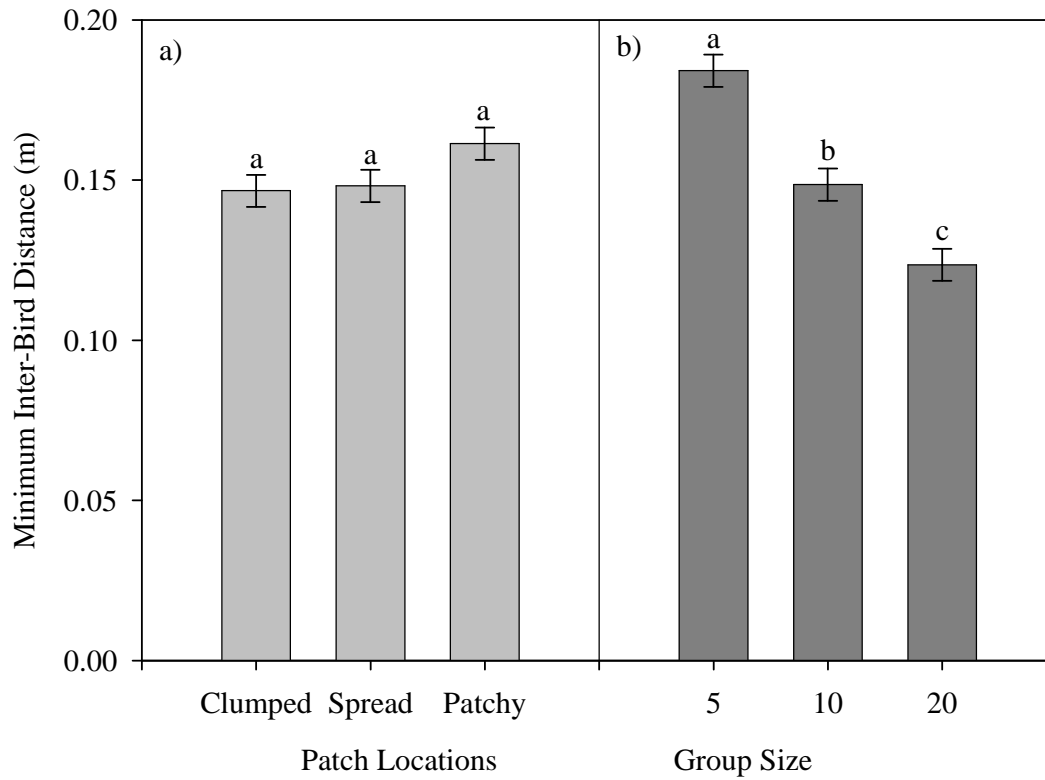
Figure 3-4. Minimum inter-bird distances by patch locations (a) and GS (b) for the free access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.

Figure 3-5. Minimum inter-bird distance deviation from random by group size (GS) for the free access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment. All bars are significantly different from zero.
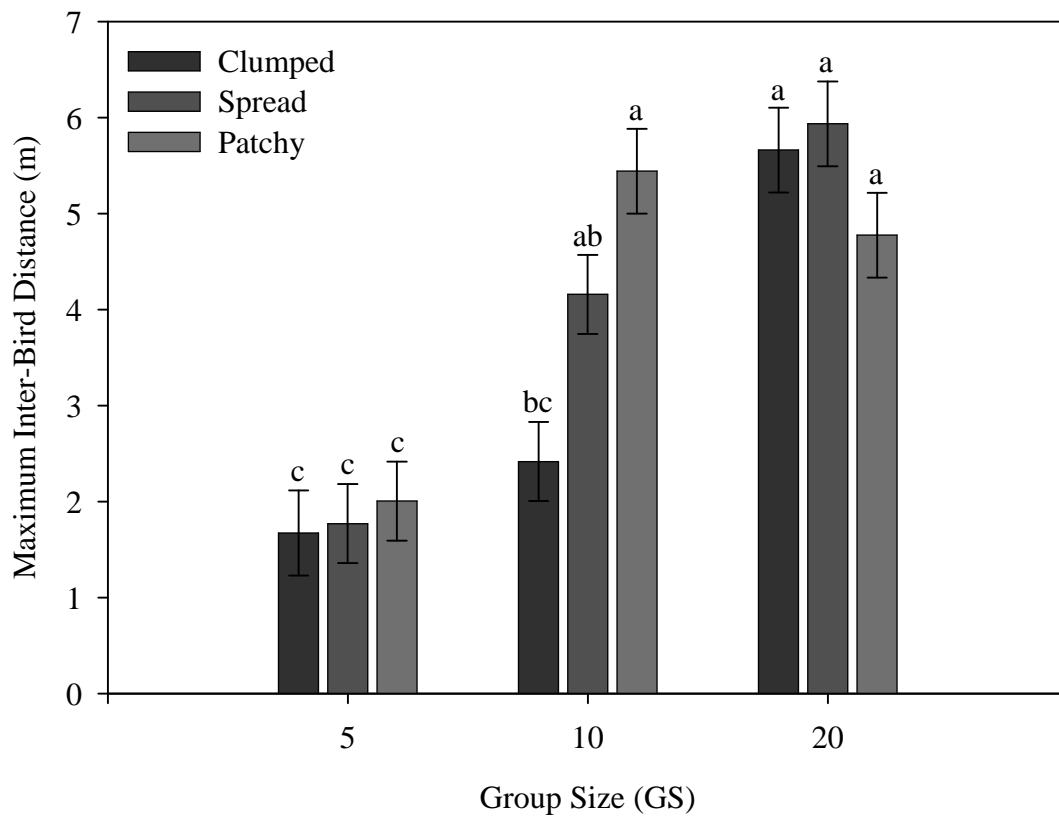
Figure 3-6. Maximum inter-bird distances according to the interaction of GS and patch locations for the free access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.
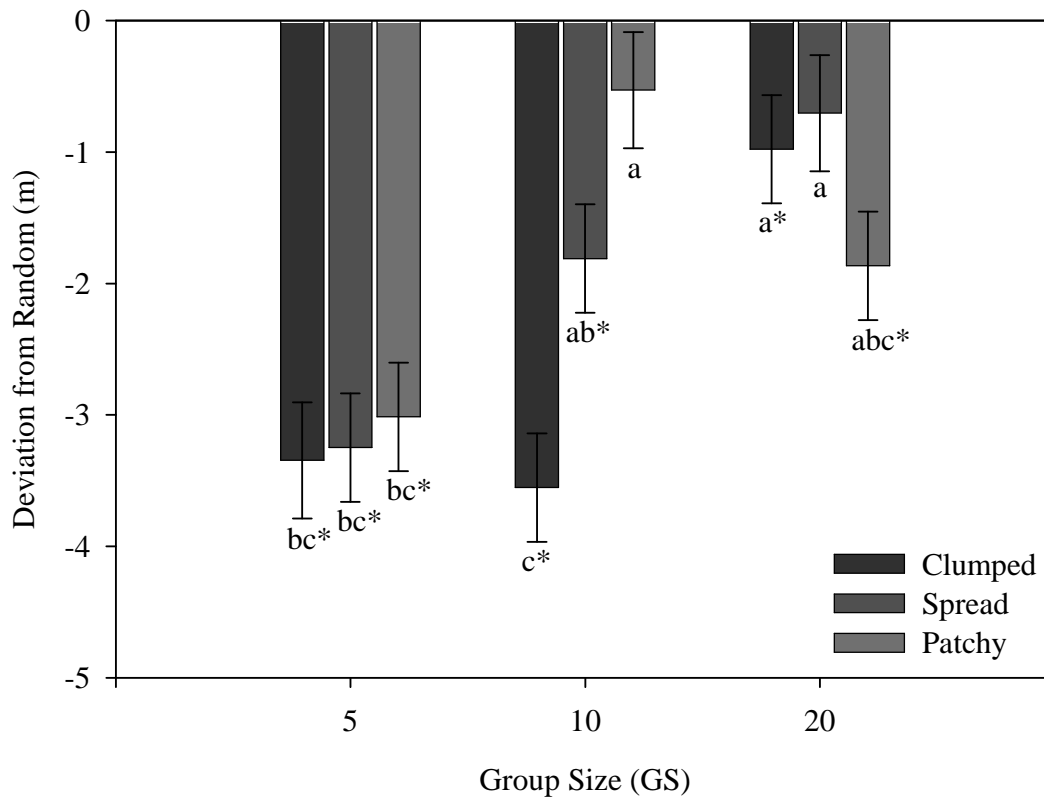
Figure 3-7. Maximum inter-bird distance deviation from random by group size (GS) and patch environment for the free access phase. Bars sharing any identical letters are not significantly different at p>0.05; Tukey's adjustment. Bars marked with an asterisk (*) differ significantly from zero.

Figure 3-8. Nearest neighbor (NN) distance according to GS for the free access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.
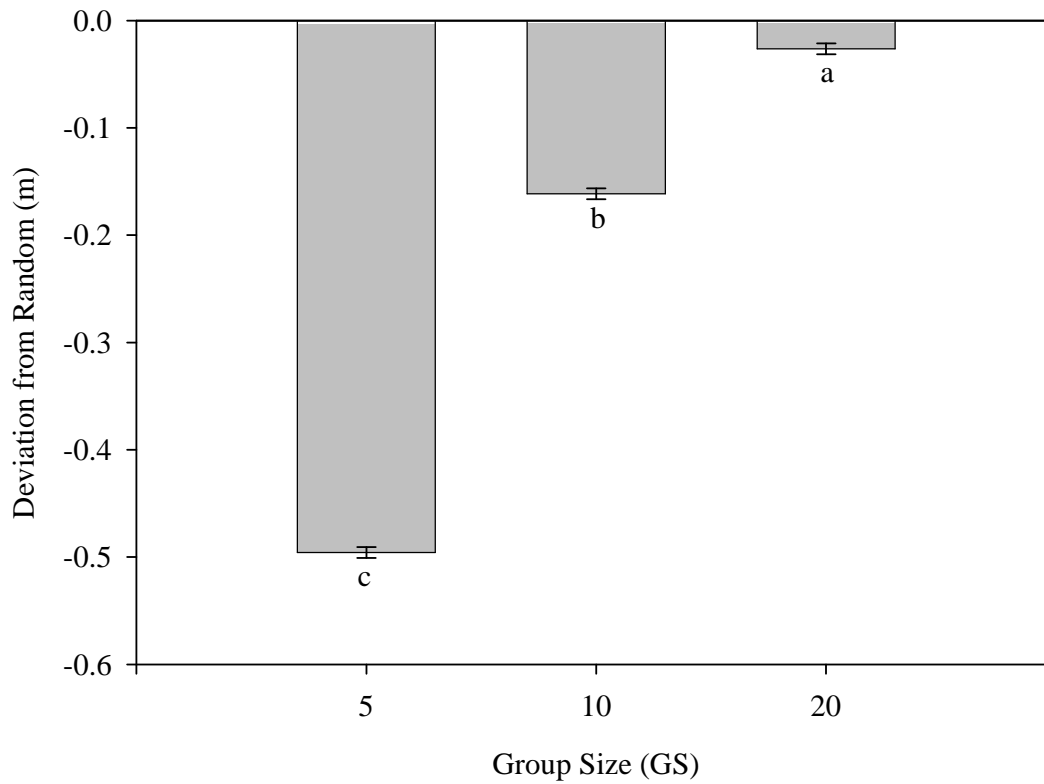
Figure 3-9. Nearest neighbor (NN) distance deviation from random by group size (GS) for the free access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment. All bars differ significantly from zero.

Restricted Access Phase

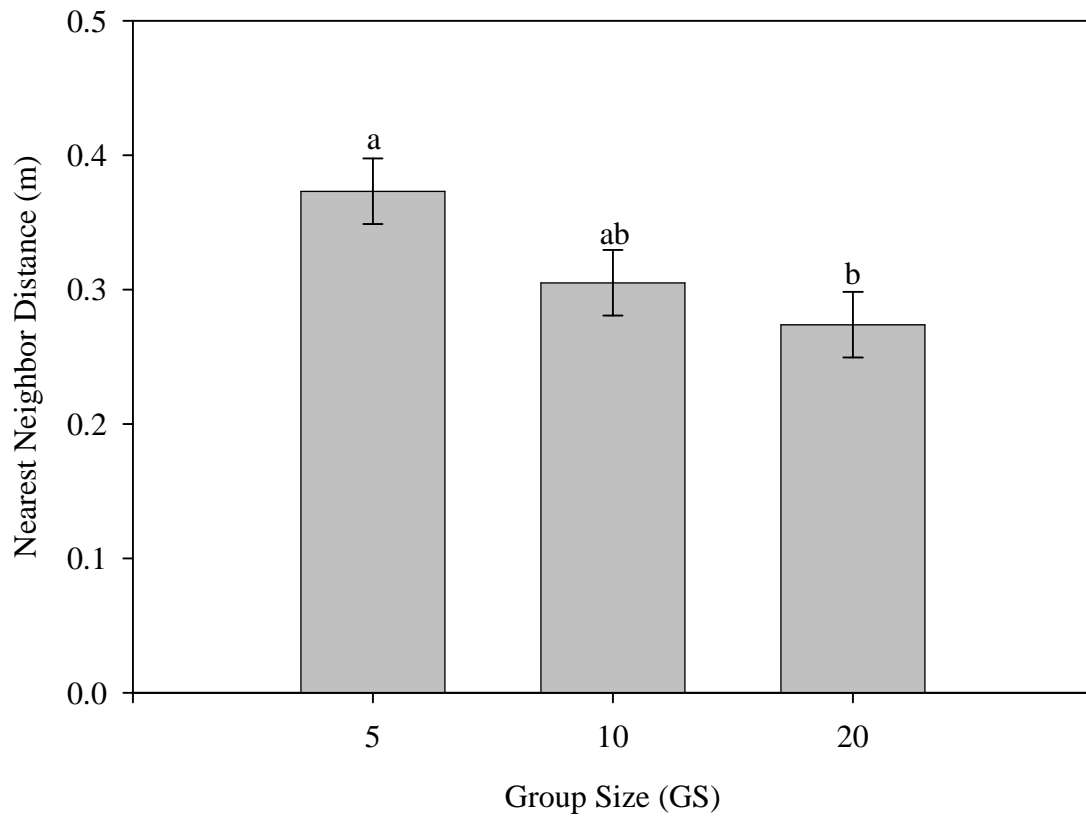<u>Individual Core Area (ICA)</u>

Neither the 30%, 50%, nor 90% core area measurements were significantly affected by GS (30%: $F_{2,56}$= 0.19, p= 0.8287; 50%: $F_{2,56}$= 0.01, p=0.9925; 90%: $F_{2,56}$= 0.47, p=0.6251), the patch locations (30%: $F_{2,56}$= 0.36, p= 0.69985; 50%: $F_{2,56}$= 0.17, p= 0.8457; 90%: $F_{2,56}$= 0.78, p= 0.4651), nor the interaction of the two (30%: $F_{4,56}$= 0.17, p= 0.9530; 50%: $F_{4,56}$= 0.31, p= 0.8698; 90%: $F_{4,56}$= 0.20, p= 0.9393).

<u>Total Core Area (TCA)</u>

The 30% group home ranges were significantly affected by patch locations ($F_{2,56}$= 7.02, p=0.0234; Fig. 3-10a) but not GS ($F_{2,56}$= 1.24, p=0.3380). The interaction of the two was also not significant ($F_{4,56}$= 0.35, p=0.8426). The 50% group home range areas were also
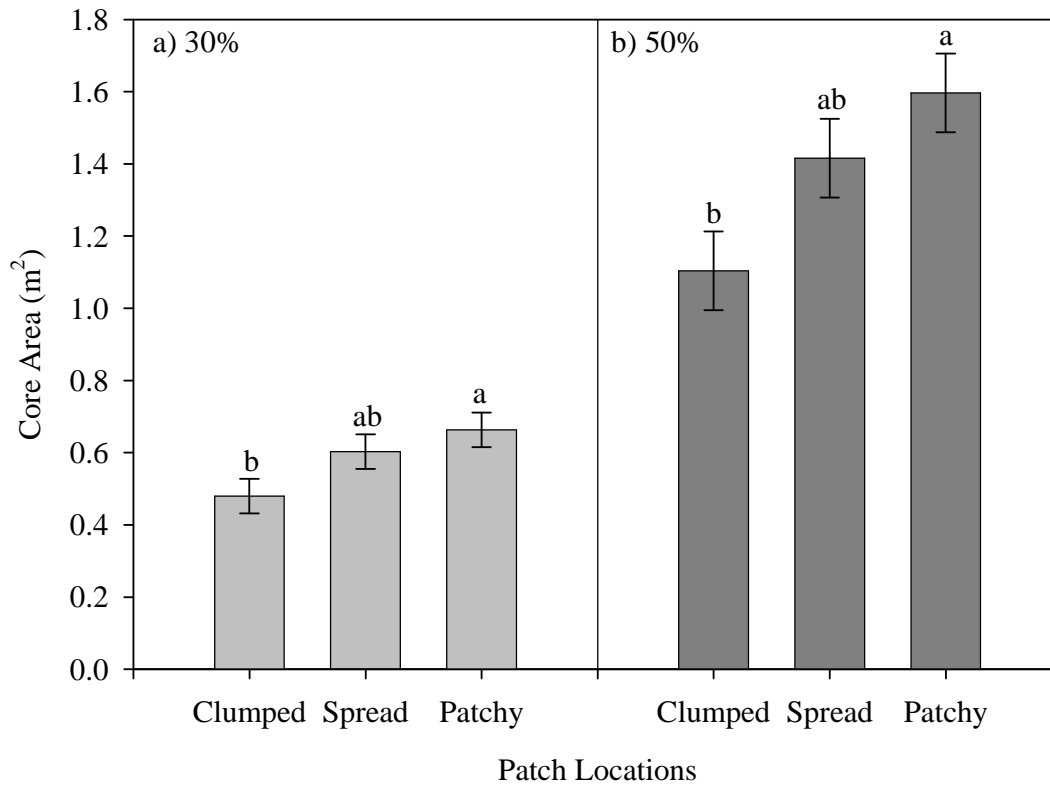
Figure 3-10. Total core area (TCA) measurements at 30% (a) and 50% (b) for the restricted access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.
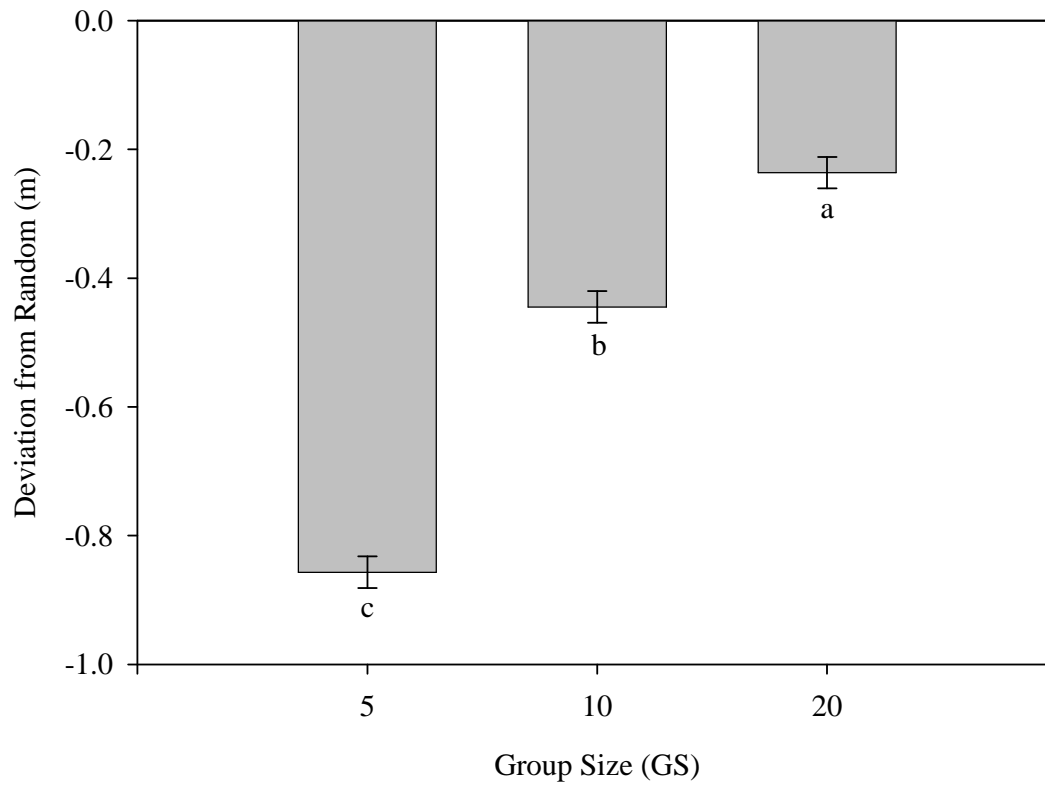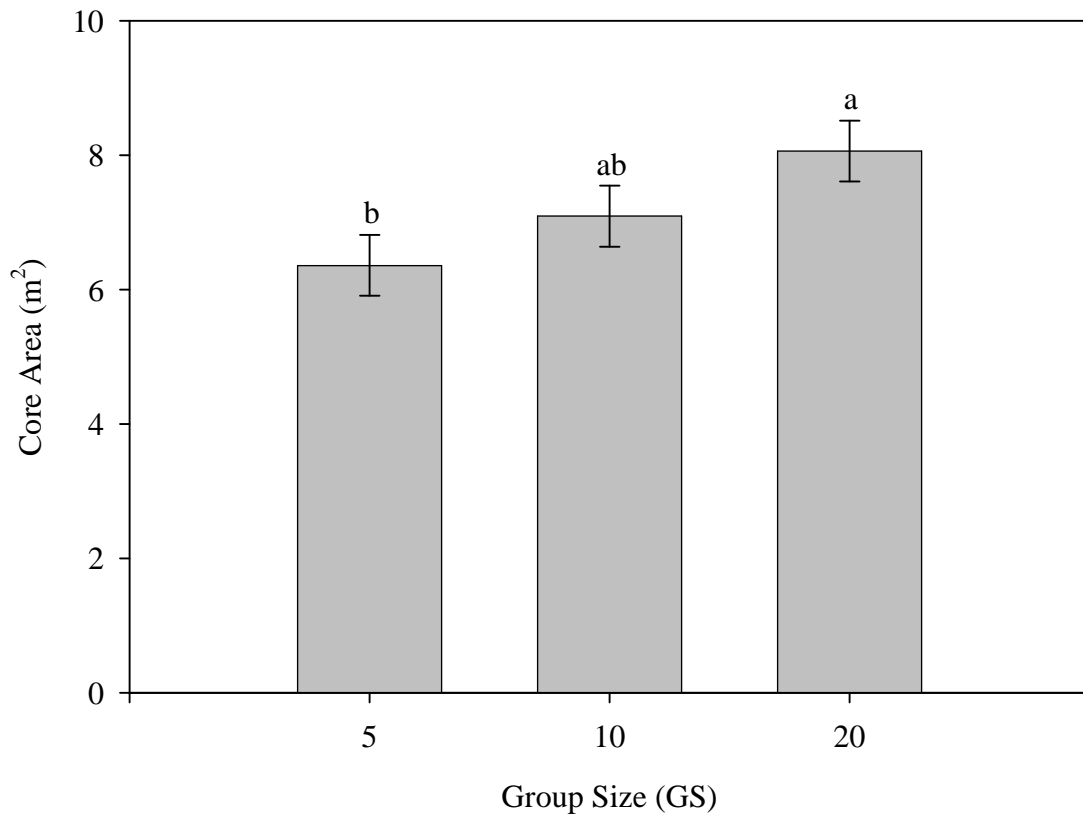
Figure 3-11. Group size effects on the 90% total core are (TCA) areas for the restricted access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.

affected by the patch locations ($F_{2,56}$= 5.02, p=0.0099; Fig. 3-10b) and again not by GS ($F_{2,56}$= 1.10, p= 0.3407) or the interaction ($F_{4,56}$= 0.59, p= 0.6716). GS significantly affected the 90% TCA ($F_{2,56}$= 3.84, p= 0.0274; Fig. 3-11), but patch locations did not ($F_{2,56}$= 2.81, p= 0.0689). There was no effect of the interaction of patch locations and GS ($F_{4,56}$= 0.11, p= 0.9775).

Inter-Bird Distances

The minimum inter-bird distance was significantly affected by the interaction of GS and patch locations ($F_{4,56}$= 3.24, p= 0.0184; Fig. 3-12). Because both the main effects of GS ($F_{2,56}$= 60.62, p< 0.0001) and patch locations ($F_{2,56}$= 7.62, p=0.0012) were also significant and produced higher F values we have discussed main effects. The deviation from random for the minimum inter-bird distance was significantly affected by the interaction of GS and patch locations ($F_{4,56}$=3.54, p=0.0121; Fig. 3-13) however the main effects of GS ($F_{2,56}$=934.89, p<0.0001) and patch locations ($F_{2,56}$=7.50, p=0.0013) were greater. The maximum distance between two birds was only significantly affected by GS ($F_{2,56}$= 48.74, p< 0.0001; Fig. 3-14), not patch locations ($F_{2,56}$= 0.73, p= 0.4880) or the interaction of the two ($F_{4,56}$= 0.24, p= 0.9126). The deviation from random for the maximum inter-bird distance behaved similarly, with a significant effect of GS ($F_{2,56}$=12.00, p<0.0001; Fig. 3-15) and non significant effects of patch locations ($F_{2,56}$=0.73, p=0.4864) and the interaction term ($F_{4,56}$=0.23,

p=0.9203). NN distance was significantly impacted by GS ($F_{2,56}$ = 23.26, p< 0.0001; Fig. 3-16) but was not affected by patch locations ($F_{2,56}$ = 1.82, p=0.1720) or the interaction of GS and patch locations ($F_{4,56}$ = 1.21, p=0.3172). The deviation from random for the NN distance was again significantly affected by GS ($F_{2,56}$=70.10, p<0.0001; Fig. 3-17) but not patch locations ($F_{2,56}$=1.72, p=0.1877) or the interaction ($F_{4,56}$=1.36, p=0.2610).

Patch Consumption

All groups nearly depleted the available food. The average percent of total patch consumption was influenced by GS ($F_{2,63}$= 4.09, p= 0.0214) but not by the patch locations ($F_{2,63}$= 1.48, p= 0.2348) or the interaction of the two factors ($F_{4,63}$= 1.31, p= 0.2744). GS_{10} consumed 99.9 ± 1.81% of the available resources, which was significantly greater than GS_5 who consumed 93.2 ± 1.81% (t=2.59, p=0.0318). Neither GS_5 nor GS_{10} were significantly different from the 99.2 ± 1.81% consumed by GS_{20} (p > 0.05).
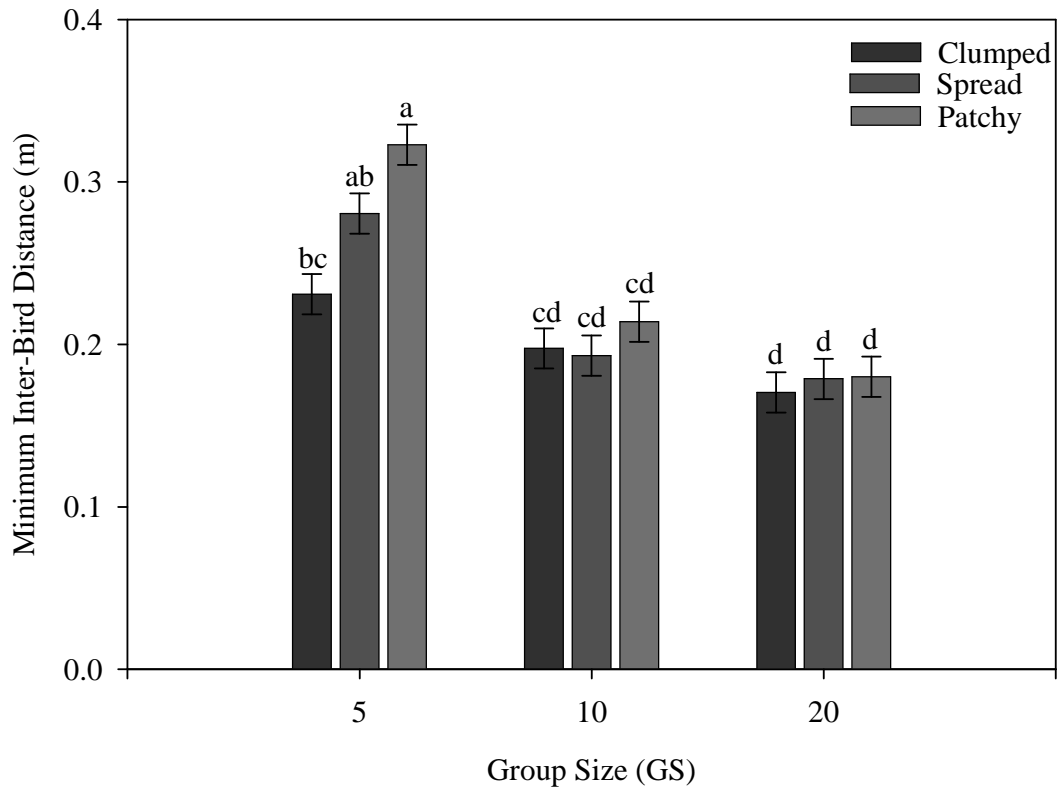
Figure 3-12. Minimum inter-bird distances according to the interaction of GS and patch locations for the restricted access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.
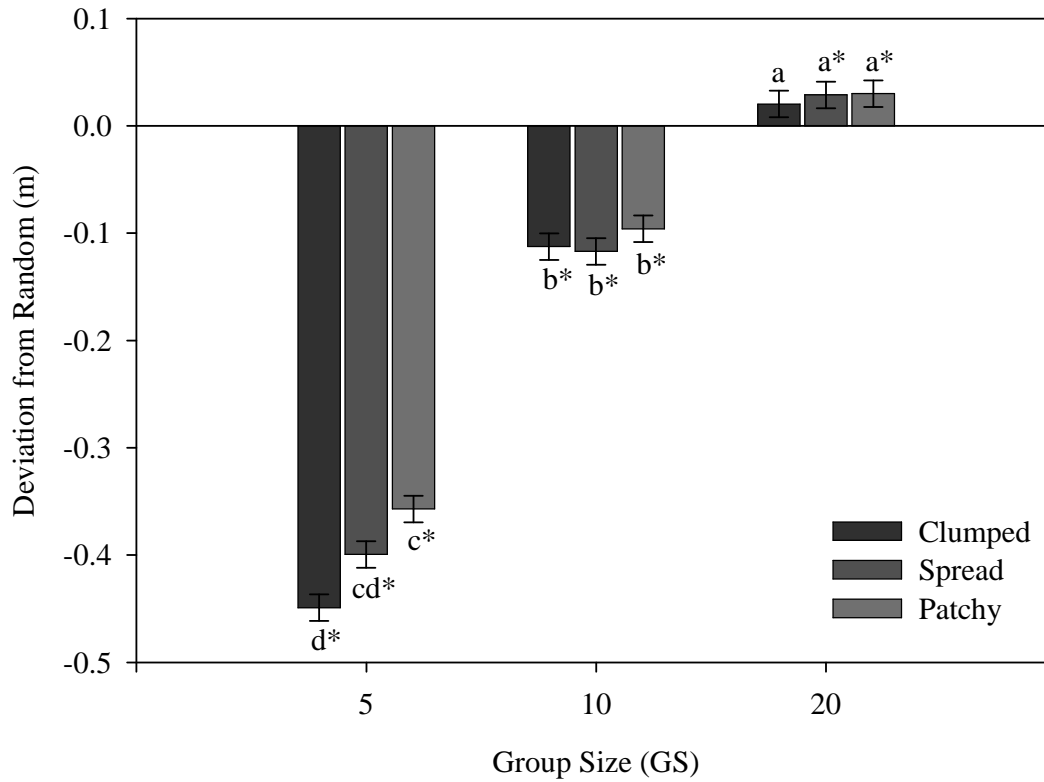
Figure 3-13. Minimum inter-bird distance deviation from random by group size (GS) and patch location for the restricted access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment. Bars designated with an asterisk (*) differ significantly from zero.
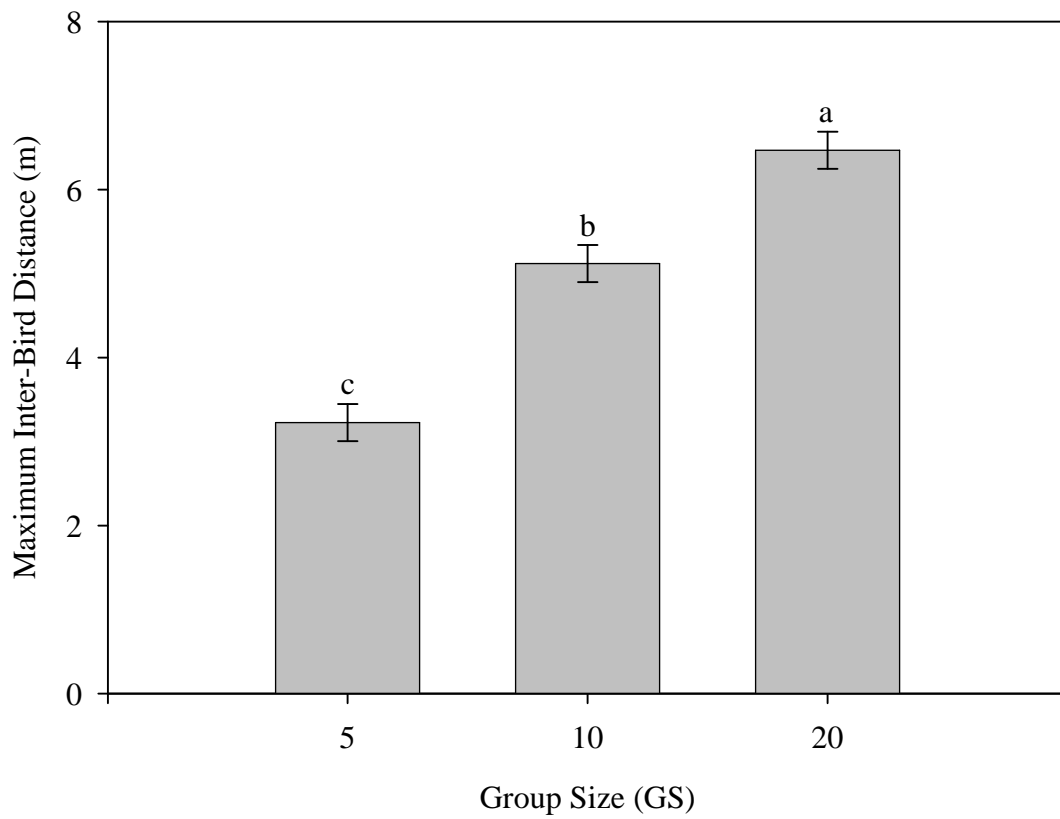
Figure 3-14. Maximum inter-bird distances, by GS for the restricted resource access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.
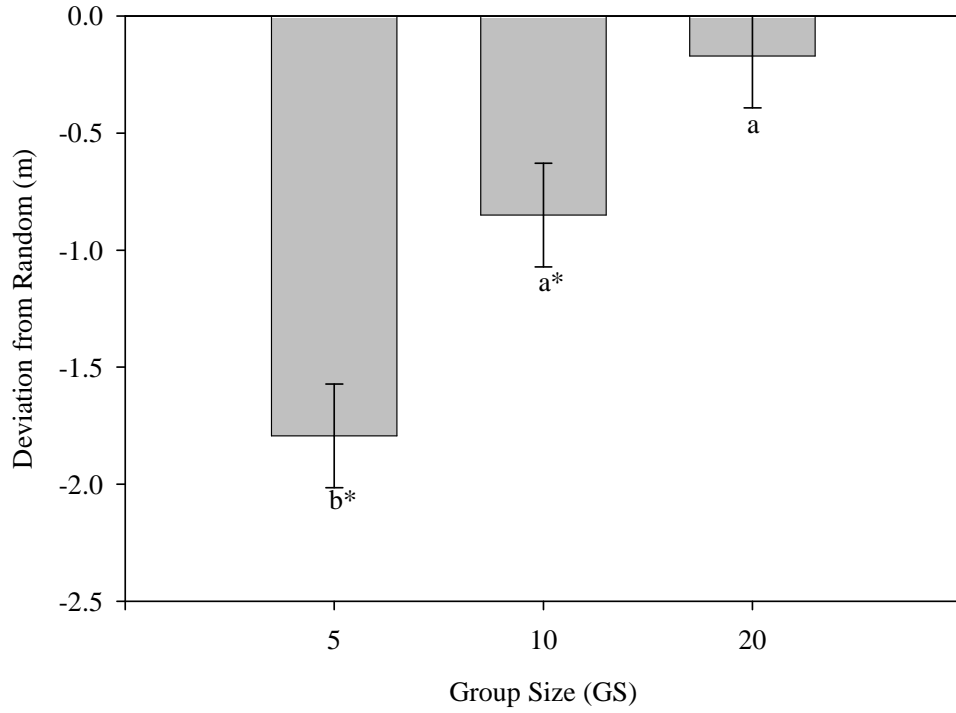
Figure 3-15. Maximum inter-bird distance deviation from random by group size (GS) for the restricted access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment. Bars marked with an asterisk (*) differ significantly from zero.
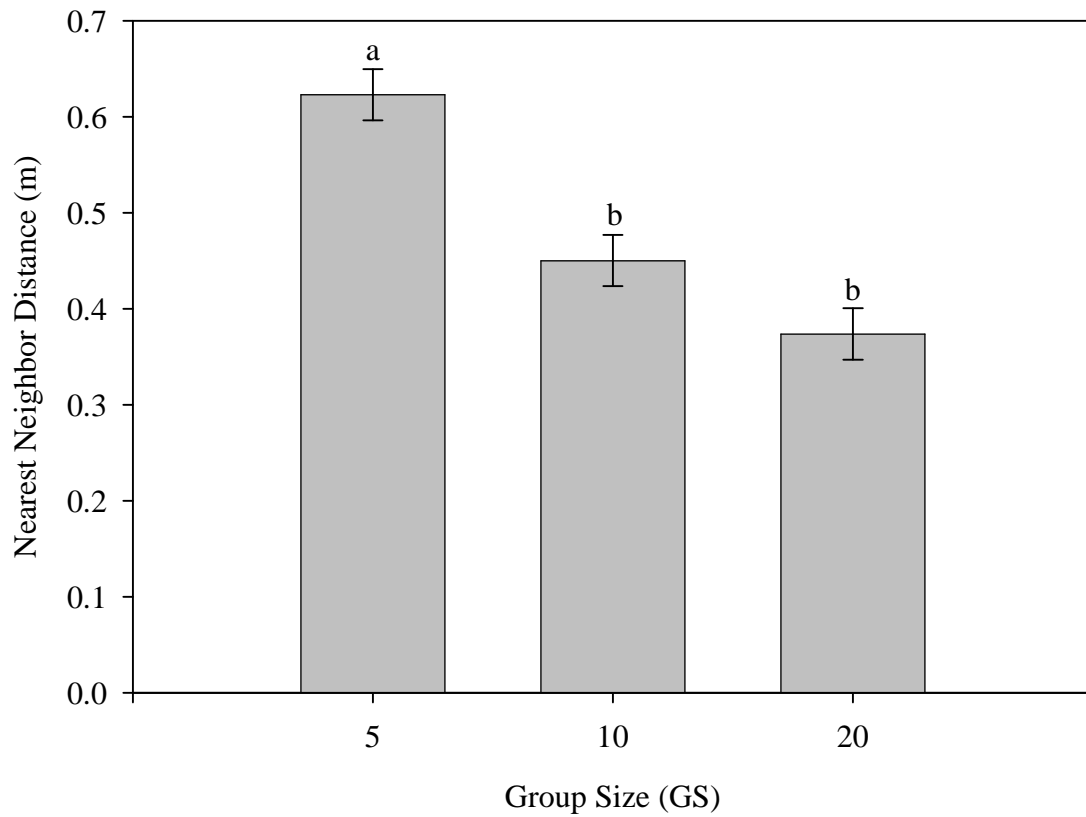
Figure 3-16. Nearest neighbor (NN) distances separated by GS, from the restricted access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.
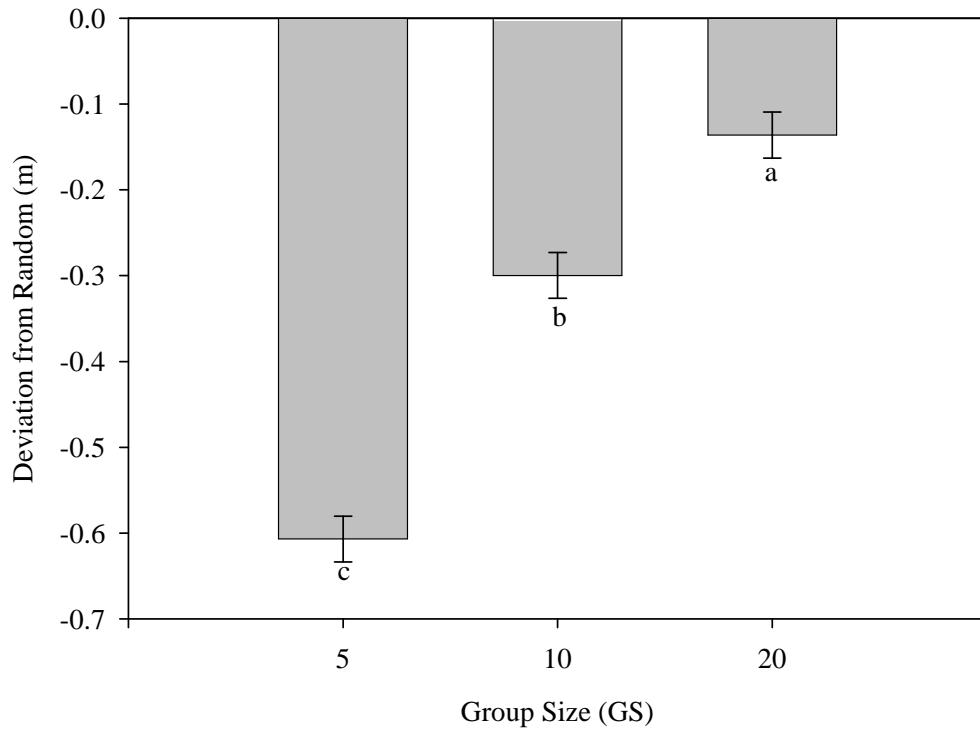
Figure 3-17. Nearest neighbor (NN) distance deviation from random by group size (GS), for the restricted access phase. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment. All bars differ significantly from zero.
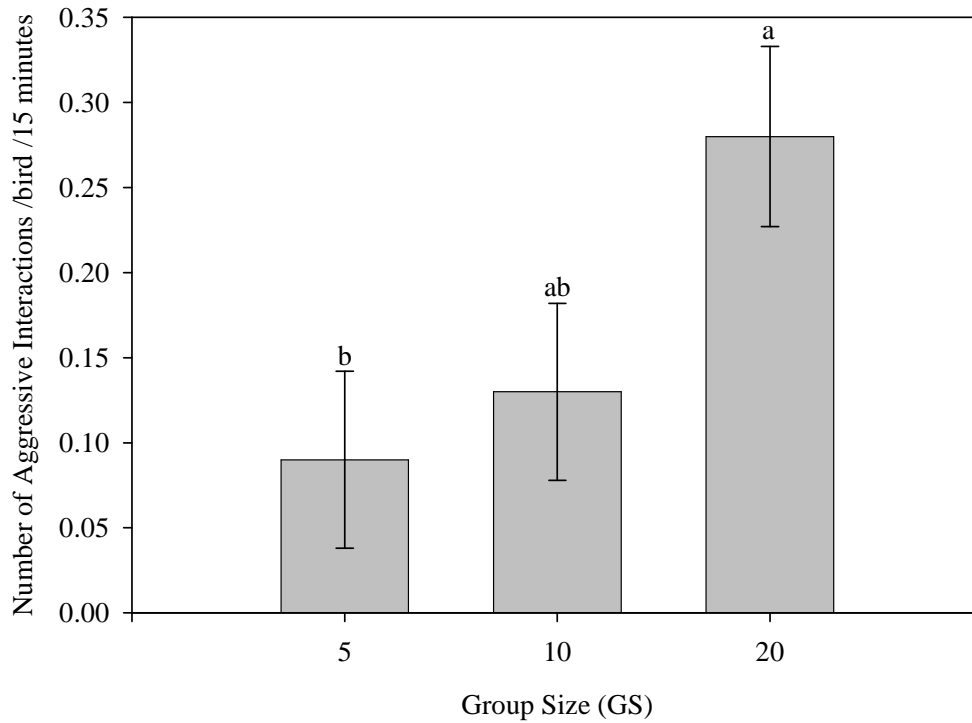
Figure 3-18. Effects of group size on the number of aggressive interaction in the restricted access phase per bird and 15 minute observational period. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05; Tukey's adjustment.

<u>Aggression</u>

GS was the only factor that significantly affected aggression ($F_{2,60}$= 5.23, p= 0.0081; Fig. 3-18). Generally aggression increased with GS. Patch locations ($F_{2,60.4}$= 0.62, p= 0.5430), order of observation ($F_{2,7.88}$= 0.28, p= 0.7629), and the patch treatment by GS interaction ($F_{4,60.1}$= 0.28, p= 0. 8912) effects were all non-significant. All interactions involving order of observation were also insignificant.

Discussion

The ICA at the 50% level was significantly affected by the patch locations when birds were granted free patch access. ICA was largest within the patchy treatment (four periphery patches) and smallest in the spread treatment (two patches equidistance from the center). GS effects were not significant on ICA at any level in either the restricted or free access phase. Patch locations were nearly significant on 90% ICA suggesting an influence of patch location on individuals' larger range of movement in the free access phase. When access to resources was restricted to a single individual, the 30%, 50%, and 90% ICA did not differ across GS or resource distribution scenario. Under these restricted conditions neither spatial clumping, nor competitor density altered the amount of space used by individual birds.

Previous works have analyzed the movements and use of space of domestic species and have established that animals are influenced by the social effects of dominance hierarchies (reviewed in Grigor et al. 1995a), and the availability of space

(Newberry & Hall 1990; Freed 2003). Space can be limited by pen size (Newberry & Hall 1990; Estevez et al. 1997), group size (Channing et al. 2001) or stocking density (Estevez et al. 1997; Carmichael et al. 1999). Channing et al. (2001) studied the effects of colony size on spatial distribution while maintaining constant densities and found no effect of colony size; birds used equal proportions of available space. Freed (2003) distinguished between social and environmental effects on home pen core areas with domestic fowl, and found that the most influential factor for bird movement was the amount of free space available within the pen. Because pen size was equal for all patch location treatments and to all experimental GS it could be the factor determining ICA, even though birds never used the entire pen.

Unlike ICA, TCA in the free access phase were mostly determined by experimental GS and not by patch location. This result is not at all surprising. If birds required a more or less constant amount of space to perform their daily routines then 20 birds would obviously occupy a greater area than five, and the dispersal of the five focal individuals should logically be greater at larger GS. Interestingly TCA in the second phase, when access was restricted to a single individual, differed according to patch location for the 30% and 50% core areas but not for the 90% level. It appeared that at these smaller levels, which measured concentrated pen use, birds in all GS used similar total amounts of space. The 90% TCA in the restricted access phase were not affected by patchiness, rather only by GS. This switch between significance of patch environments and GS suggests that this greater extent of pen use was more significantly affected by GS than the location of patches. The 90% TCA represented the spread of the focal birds within the pen and were expected to increase with GS.

Birds did not appear to distribute evenly across all GS and in fact birds in different GS responded differently to patch locations in both the free and restricted access phase. When birds were provided free access to resources, patch environments significantly affected minimum inter-individual distances, a measure of the closest individuals. This reflects our expectation that patchiness should influence, and increase inter-bird distances. Under restricted access the minimum inter-bird distances were not affected by the patch environment for GS_{10} and GS_{20}, but significantly increased with patchiness for GS_5. For this GS minimum distances were shortest in the clumped environment and longest in the patchy environment. Again this finding was expected, and it is understandable that smaller GS would be more significantly affected by environmental conditions than larger GS. Smaller GS afford individuals less predator avoidance than large groups and thus environmental conditions should play more of a role in shaping the behavior of these smaller groups (Pulliam 1973).

In both phases we observed an overall decrease in minimum and NN distances as GS increased. This trend of decreasing distances with increasing GS was predicted from the random simulation based on the pen dimensions. We expected smaller GS to have a greater deviation from these random values than the larger GS, and in fact this is what we found. Concerning the minimum inter-bird distances in the restricted access phase both GS_5 and GS_{10} were significantly smaller than random, while GS_{20} was significantly larger than random. This suggests that the larger GS was farther apart than randomly expected. Flock cohesion, as measured by NN distances, increased with increasing GS while the deviation from random decreased with

increasing GS. While the physical distance between birds decreased as GS increased, larger flocks were closer to random expectations than smaller ones; smaller flocks clumped to a greater degree. In both the free and restricted access phase GS_5 NN distances were significantly larger than GS_{20}, which was the opposite of what we expected. The results of both minimum inter-individual and NN distances are counterintuitive and seem to be inconsistent with expected foraging strategies predicted for the different GS used in this experiment. Birds from larger groups were expected to maintain larger inter-individual minimum, maximum and NN distances compared to birds in smaller GS. While maximum inter-individual distances did increase with GS in both phases, minimum inter-individual and NN distances decreased with GS. However while the actual distances between birds were different than what we expected, we did find that the deviation from randomness was greater for smaller groups. While the risk of predation decreases as GS increases (Lima 1995), the level of competition for resources also increases between group members (Clark & Mangel 1984). We expected to find an increase in inter-individual distances with GS as birds attempted to minimize resource competition. Likewise, because the risk of predation is larger for small groups, we expected that smaller GS would maintain smaller inter-bird distances. In support of our original expectation is the fact that the minimum inter-bird distances for GS20 were greater than random expectations while distances for the two smaller GS were smaller.

Other studies have demonstrated that birds distribute themselves farther apart whilst foraging, and maintain closer contact with flock members when performing behaviors such as resting and preening (Keeling & Duncan 1991; Keeling 1994;

Keeling 1995). GS_5 individuals had the greatest opportunity to feed from patches, as each individual had a maximum of four competitors while individuals from GS_{20} had a maximum of 19. Because individuals from larger GS encountered a higher level of competition when attempting to gain access to resources, some may have given up attempts to forage and therefore resigned to performing other behaviors. Any behaviors other than foraging, such as standing, resting, or preening are performed at closer distances than foraging (Keeling & Duncan 1991). If individuals were predominantly not engaged in foraging behaviors in larger GS because of the increased competition, then NN and minimum inter-individual distances should decrease as GS increased. This difference in inter-bird distances based on behavior may explain why minimum and NN distances behaved against to our original expectations.

Maximum inter-bird distances measured group spread, and were unequally influenced by patchiness when comparing free versus restricted access phases. Under free access patch locations did not affect the dispersal of GS_5 and GS_{20} individuals, while those from GS_{10} were farthest apart in the patchy, and closest together in the clumped environment. In the second phase, when patch access was restricted, only GS significantly affected maximum inter-bird distances. Not surprisingly maximum inter-bird distances increased with GS, as 20 equally spaced individuals should take up more pen space, thus the distance between the two farthest individuals should be greater at this GS than that of five individuals. From an ethological perspective larger flocks should have greater dispersal, or larger maximum inter-individual distances than small flocks. Because flocking reduces predation risk, and the degree of

protection is directly related to group size (Lima 1995) then smaller flocks are more vulnerable than large flocks, and the two farthest group members should be closer together in smaller rather than larger GS. This difference in maximum inter-bird distance would also happen if birds maintained a constant distance between them, but they did not. Furthermore because competition increases with increases GS larger group should place more distance between themselves and group members in an effort to reduce this foraging competition.

Previous work on patch locations has focused on the productivity and welfare of laying hens in battery cages in relation to the orientation of feed troughs (reviewed in Craig & Adams 1984, and in Mench & van Tienhoven 1986). Other experiments have investigated social effects, rather than group size effects per se, on resource use and movements (Mankovich & Banks 1982; Banks 1984). Indications of social dominance effects were not detected in the present experiment as many individuals gained resource access in both restricted and free access phases (personal observation). When birds had free access to patch resources no significant differences in aggressive resource defense strategies were detected across either GS or patch locations. Furthermore, patch locations played no role on how much food the birds consumed. But we observed increased aggression with GS when birds were forced to compete for limited access to patches. This is similar to the findings of Mench (1988) who determined that aggression in broilers increased when access to resources became limited. With access restricted to a single individual, at any given time more birds were excluded from eating in the larger GS than in the smaller ones. Thus a greater number of individuals remained hungry and had to wait to gain patch access.

This explained the increase in aggression with GS, not because birds were defending resources (in fact the smaller GS had a better opportunity to guard distributed patches), but rather aggression in this case seemed related to scramble competition strategies used to gain access to patches.

There was an overall effect of patch location on the inter-bird distances in both the restricted and free patch access phases, but once again these results were not consistent across all GS for all measurements. When patch access was restricted GS, or the number of competitors, was important for both aggressive strategies and resource consumption. The level of competition had important consequences on group cohesion, or NN distances, and how individuals dispersed within the available space. With respect to TCA and maximum inter-individual distances groups adopted different foraging strategies in accordance with the number of competitors in the free access phase. In the restricted access phase patch locations dominated TCA for the two smaller levels (30% and 50%) while increasing GS, or competitor density, predicted the 90% TCA.

The patchiness of an environment was found to influence how domestic fowl used the available space as well as the inter-individual distances maintained. Furthermore patch location affected GS differently. Birds showed less aggression in the free access phase than in the restricted phase, which is in accordance with other studies on broiler chickens (Mench 1988). GS was the most significant factor for inter-bird distances; however GS responses were not uniform across patch locations. The effects of induced competition as a result of limited access had a profound effect on bird behavior.

Results of this experiment demonstrate that the dispersal of food resources as well as the accessibility of those resources has an impact on how animals use the space available to them and flock cohesion. Furthermore this experiment demonstrated that these effects are interdependent with the effects of GS. A better understanding on how animals use their space and identification of limiting factors can have important repercussion for the welfare and performance of domestic fowl.

Chapter 4: Evidence of Optimal Foraging Strategies by Domestic Fowl (*Gallus gallus domesticus*)

Abstract

The behavior of domestic fowl was compared to the predictions of optimal foraging theory and specifically marginal value theory as applies to a patchy environment. Birds were tested in three group sizes to further examine the mediating effects of group size on foraging behavior. Despite generations of intense artificial selection pressures birds continue to forage in an energy-conservative manner. In a three-patch discrimination trial birds consumed significantly more food with increasing patch quality. Larger group sizes consumed the greatest amount of food, suggesting that resource monopolization did not occur. The number of foraging bouts, as well as individuals foraging, also increased with patch quality and group size. Foraging duration, or patch residence time, increased with patch quality but decreased with increasing group size. Aggression increased with patch quality but was not affected by group size. Finding showed that birds are capable of discerning patch quality based on the amount of work required to obtain a food reward, and adjust this foraging strategy according to the number of competitors present.

Introduction

Optimal foraging predicts that an animal will forage in a manner that maximizes its net energy gain (Charnov 1976; Caraco 1981). When confronted with a patchy environment, the amount of time an animal spends foraging, patch residence time (PRT), as well as food consumption will increase with patch quality (McNair 1982; Alonso et al. 1995). Optimal foraging decisions require that an animal not only be able to determine the average patch quality within its environment, but also readily distinguish between patches of different quality. Patch quality may differ in the obvious sense that patches vary in the total amount of resources available. However, it is possible that when sharing identical resource quantities patches differ in resource accessibility and thus generate different foraging efficiency potentials. If resources are more difficult to access and consume then foraging efficiency is diminished and animals must spend more time and energy in pursuit of resources. Animals must not only determine the abundance of resources within a patch but must further differentiate between patches according to the maximum net energy gain per unit time possible. Research has repeatedly shown that wild species are able to discriminate and accurately choose patches based on resource availability, nutrient quality, and net energy gain (Lewis 1980; Caraco et al.1989; Valone & Giraldeau 1993; Alonso et al. 1995; Kie 1996; Alm et al. 2002; Kacelnik & Brunner 2002; Schaefer et al. 2003).

For many species foraging strategies are significantly affected by group dynamics. When patches are scattered and unpredictable, individuals improve their efficiency by foraging in groups; however this success depends heavily on patch density, and level of competition (Clark & Mangel 1984; Carco et al.1989). Information about the

availability of resources within an environment increases with flock size (Clark & Mangel 1984), as the chances for finding resources increases. Considered as a whole, the group possess a greater amount of information than any single individual. Group members, therefore, monitor the foraging of others in order to capitalize on rewarding information (Clark & Mangel 1984). However group dynamics predict that not all members will enjoy the same feeding rate. When resources are discovered, dominants will attempt to monopolize access and thus improve their foraging outcomes in relation to subordinates. Stahl et al. (2001) found that subordinates search at a faster rate and mainly occupy the front edges of the foraging flock while dominant individuals displace subordinates once patches are discovered. Even without hierarchical competition the number of individuals present at a patch, all attempting to feed, will create scramble competition. As compared to resource defense and monopolization scramble competition occurs when group members all compete simultaneously, not to defend or monopolize, but merely for access to resources. This behavior is likened to an 'every-man-for-himself' strategy. Without the ability to control access to resources all birds will attempt to consume as much of the available resource as possible, as quickly as possible (Emlen & Oring 1977; Robb & Grant 1998; Estevez et al. 2002). This scramble competition, which may lead to an increase in aggression, is different from true resource defense. Rather than competing to control access to resources individuals are vying with others to merely gain access to the contested resource.

While the ability to forage optimally in patchy environments and group contexts is well documented in studies of wild species from natural environments, limited work has focused on the current discriminating ability of domestic animals. Many domestic

species have been shaped by generations of intense artificial selection geared towards increasing growth and productivity-related traits (Dumont & Petit 1998; Gustafsson et al. 1999; Arcis & Desor 2003). This selection, based almost exclusively on performance, has introduced a myriad of morphological and physiological changes (Jones et al. 1980; Mench & van Tienhoven 1986; Jackson & Diamond 1996; Rauw et al. 1998; Bokkers & Koene 2003). In addition to, and possibly resulting from the physical changes incurred through the process of domestication, behaviors have been altered (Mench 1988; Braastad & Katle 1989; Savory & Mann 1997; Rauw et al. 1998; Schutz et al. 2001). Newberry (1995) argues that these may to some extent be necessary. Modifications would enable the animal to adjust its behavior according to the transition from a natural environment to a production situation in which food and shelter are readily available and the risk of predation is minimal or non-existent. Therefore, it may be expected that domesticated species would progressively become less efficient in their foraging strategies. If natural selection no longer acted on foraging strategies and behavior domesticated species may cease to operate according to optimal foraging predictions. Without exposure to patches or a variety of foods, and the pressure of natural selection to readily distinguish between them, foraging efficiency may become relaxed over a number of generations.

Recent work with domesticated species demonstrates that despite massive artificial selection pressures the behavioral repertoire of domestic animals remains intact in relation to their wild ancestors. Changes that have occurred are confined to differences in frequency of expression. A number of these studies have demonstrated that, in the absence of natural selection pressures, a significant relaxation has occurred in the

willingness of domestic species to work for food. For example, domestic pigs demonstrate adjusted expressions of feeding behavior when compared to wild boars. Gustafsson et al. (1999) found that domestic pigs stayed at patches longer, and had fewer overall sampling visits to available patches when compared with wild boars. Similar results have been found in domestic fowl (Andersson et al. 2001; Schutz & Jensen 2001; Schutz et al. 2001). Schutz & Jensen (2001) demonstrated that junglefowl employ a contrafreeloading foraging strategy, which is choosing to work for a food reward when the same reward is freely available. Domestic fowl engage in significantly less contrafreeloading behaviors. Andersson et al. (2001) found that wild type individuals frequently demonstrate a more costly foraging strategy that involves more transitions between patches, and an increased number of sampling visits.

Foraging strategies that have been directly affected by artificial selection and relaxed predation and starvation pressures may not agree with optimal foraging predictions in domestic environmentals. Sampling increases an animal's fitness in naturally unpredictable environments as without it foragers may have limited knowledge of environmental quality (Arcis & Desor 2003). Artificial, or domestic, environments are predictable regarding resource location and availability of food and water. Under these conditions domestic species incur an increased cost by employing energy-demanding foraging strategies that involves frequent information gathering via sampling (Gustafsson et al. 1999; Schutz & Jensen 2001). Nonetheless, the changes reported in foraging behavior of domesticated species in artificial, predictable environments do not violate optimal foraging theory predictions. These changes appear to ultimately increase the animals' fitness under such environmental conditions and pressures.

Domestic fowl (*Gallus gallus domesticus*), descendents of the red jungle fowl (Siegel et al. 1992) provide an excellent animal model for investigating the mediating effects of artificial selection and GS on foraging behavior. Domestic fowl have been selected for large body mass and rapid growth (Jackson & Diamond 1996; Rauw et al. 1998). Under modern production settings birds are fed a uniform poultry meal from feeders distributed in a patchy but predictable fashion. While recent studies have provided clear evidence for the retention of foraging strategies by domestic fowl, little is known as to whether or not birds can discriminate between patches of varying food accessibility, to ease of consumption, rather than availability. Few have investigated the response of optimal foraging strategies to different group sizes (GS) and the ability to discern patch quality in unpredictable situations

The present study examined the foraging behavior of different GS of naïve domestic fowl in a patchy environment. Patches contained the same exact amount of an attractive food source, but ranged according to food accessibility. The accessibility of a food resource to an animal is similar to the handling effort required to obtain the food reward. We suggested that adjusted foraging strategies, appropriate in domestic environments, should not violate the predictions of optimal foraging theory. Namely, we hypothesized that birds would forage in the most energy efficient manner according to the accessibility of food as well as the number of competitors present. We predicted that discriminatory abilities remain, despite the pressures of artificial selection. The animal model we chose was a modern broiler strain that has been under notably heavier artificial selection for growth and production qualities relative to other domestic species. Despite these extreme pressures we predicted that birds could discern patch quality on the basis of

food accessibility, and subsequently opt to forage at patches requiring the least amount of effort. We also predicted a higher level of competition at the highest quality patch as GS increases. As consequence of this increased competition we expected to find a larger number of individuals foraging from sub-optimal patches at larger GS.

Materials and Methods

Facilities and Experimental Animals

This experiment was conducted at the University of Maryland's Upper Marlboro Applied Poultry Research Facility from March 17th 2003 through June 3rd 2003. A total of 336 one-day old male broiler chicks were obtained from a commercial hatchery (Allen's Farm Inc. in Seaford, DE). Upon arrival to the facility chicks were divided into eight separate pens of forty-two birds. The pens were constructed of PVC piping and black netting, measuring 1.8m x 2.4m with a floor area of 4.5m^2 covered with 5cm of wood shavings. Birds were maintained on a lighting program of 14L: 10D in an effort to promote slow growth and leg health. Temperature and ventilation programs followed commercial practices. Food and water were provided *ad libitum* through a central large tubular hopper and a line of nipple drinkers (7 nipples p/pen, 6 birds per nipple) located along one side of each pen. Feeding followed commercial practices. The diet was specifically formulated to slow growth rate, consisting of 3 phases, starter (19% crude protein, 2800.00kcal/kg metabolizable energy) and grower (17% crude protein, 2801.70 kcal/kg metabolizable energy), and finisher (19% crude protein, 3251.70 kcal/kg metabolizable energy). The starter phase was administered from

days 0-14, the grower from 15-50, and the finisher from 50 until completion of the experiment at day 79. Mortalities were recorded daily.

Birds were tagged at three weeks of age on each side of the neck using the Swiftack for Poultry Identification System (Heartland Animal Health, Inc). Circular tags were made of sturdy laminated white paper, 5cm in diameter. Numbers of solid black were printed on both sides, ranging from 1 to 35. Seven birds per pen were left unmarked as replacements in the event of mortalities. The experiment reported here took place when the birds were eight to nine weeks of age. During testing each of the eight pens of birds were divided into three experimental groups of 5 (GS_5), 10 (GS_{10}) and 20 birds (GS_{20}). Five individuals in each of the experimental GS per pen were designated, at random, as focal birds. If a tagged, non-focal bird died then a new individual was tagged with that same number. If a focal individual died we used the group member with the next highest tag number to complete the group for testing. The three experimental GS were housed together in order to create a similar background environment for each testing group, and enabled us to measure the distinct reaction of birds to a new environment.

Experimental Design

For this study we constructed three testing arenas, each measuring 2.4m x 7.3m. We covered the arena floor with 5cm wood shavings and the walls in black plastic sheeting. Water was provided *ad libitum* from 14 nipple drinkers located in two lines at each end of the arena. Two hours prior to testing birds were feed

restricted. This was accomplished by placing a white plastic bag around the food hopper to prevent access.

Resource patches were created from dark brown plastic containers, 10 cm in diameter, 14cm deep and placed on 12cm high platforms. To increase the level of competition at each patch we limited access to one individual. This was accomplished by attaching sturdy clear plastic around the patch, except for a 4cm opening on one side. Three patches were arranged in a triangular fashion, 80cm apart from one another in the centre of the arena with each opening facing the center of the triangle. All patches contained 50 grams of dry cat food, which had previously been demonstrated to be highly attractive. Varying amounts of litter: 60ml, 120ml or 180ml were mixed with the cat food to create different food accessibilities. These patches ranged in food to litter ratios from a high quality patch (HQP) with 25% to 75% litter to food, a mid quality patch (MQP) with 50% to 50% and a low quality patch (LQP) with 75% litter and 25% food. Patches containing more wood shavings required greater effort to obtain the food resource, as litter was not edible. The height of the food/litter mixture was standardized to reach the 9cm of the LQP by affixing discs inside the MQP and HQP. Another disc was placed on top of the mixture, and removed immediately following the birds release into the testing arena. The position of each patch within the triangular arrangement varied randomly.

For each test one GS was transported in crates from their home pen to a testing arena. After testing, the second GS was removed from the same home pen and transported to a different arena for testing. This procedure was repeated with

the final GS. The home pen and GS order, as well as designated testing arena, were randomly assigned. Each experimental GS was tested only once. These birds were used in a prior experiment and had been transported, in crates, from their home pens to the testing arenas for a period of nine weeks and had become acclimated to the procedure. Birds were exposed to the patches one week prior to this experiment, twice a day for three consecutive days. Patches were filled with 100g of cat food and placed in the centre of each home pen. Birds eagerly and quickly consumed all of the available food and considerable numbers of birds would gather around the patches (personal observation). The Institutional Animal Care and Use Committee at the University of Maryland approved this experimental protocol (R-03-04) prior to the beginning of testing.

Measurements

For each experimental trial a 30 min. observation period was video recorded for later analysis using the Observer (v.4.1 Noldus). From these videos we collected the identification number (ID) of each bird at each foraging patch (HQP, MQP and LQP), and calculated average foraging durations and total patch residence time (PRT). We defined foraging durations as the length of time during which the fowl had its head inside the patch. PRT encompassed the total amount of time a patch was occupied during the 30 mins. Each time a bird's head passed through the patch opening it was counted as a foraging bout regardless of whether it was the same bird successively or different individuals. At 1 min. intervals (from 1 to 30 min.) we collected the total number of birds located within the patch area, defined by the 5 cm area surrounding each patch. In addition, we recorded

all aggressive interactions that occurred at a patch by individual IDs. Aggressive interactions that occurred outside of the 5cm patch diameter were not recorded. Aggressive definitions were modified from Estevez et al. (2002) and consisted of pecks, threats, leaps, kicks, fights and fights with pecks. To determine patch resource consumption the patches were weighed prior to and after each testing session.

Statistical Analysis

All analyses were conducted using Mixed Model ANOVA in SAS statistical analysis software (v. 8.1, SAS Institute, Cary, NC). Model assumptions of normality and homogeneity of variance were examined. The number of individuals foraging from each of the HQP, MQP and LQP patches and the number of aggressive interactions were log transformed while the total number of patch foraging bouts and total patch consumption measures were square root transformed. In addition, variance components were separated by patch for the PRT analysis in order to meet the assumptions of homogeneity of variance. All data was analyzed by a Mixed model with experimental GS and patch quality as fixed factors with pen as a random blocking factor. A Kronecker product was incorporated, generating covariance matrices to account for multiple dependencies in variables. This design enabled two variance matrices to be calculated, an unstructured matrix and a compound symmetry matrix. The unstructured matrix accounted for the random block effect of pen, while the compound symmetry matrix accounted for the repeated-measure dependence of the patch treatment response variables, as all three patch treatments were

presented in cafeteria (multiple choice) style. Because of the low occurrence of aggressive behaviors, a variable composed of total aggression noted was modeled for statistical analysis. Total aggression was measured as the sum of all aggressive interactions per 30 minute testing session, on a per bird basis. Mean comparisons were according to Tukey's LSD adjustment for Type I error rates (for review see Jones 1984).

Results

Patch Resource Consumption

The total patch resource consumption (Fig. 4-1), measured as the difference between pre-trial and post-trial weights, was significantly affected by both GS ($F_{2,21}$=4.66, p=0.0212) and patch quality ($F_{2,20}$=20.61, p<0.0001) but not by the interaction of the two ($F_{4,23.2}$=0.73, p=0.5791). A posteriori contrasts revealed a significant difference in the amount of food consumed at both the MQP and LQP between GS_5 and the larger two, GS_{10} and GS_{20} (t=3.07, p=0.0059).

Number of Foraging Bouts and Distinct Foraging Individuals

Recording individual bird ID's enabled us to examine if the total number of distinct individuals (visitors) foraging at patches differed between GS and/or between patches (Fig. 4-2). GS and patch quality had significant effects on the total number of distinct individuals foraging ($F_{2,20}$=17.73, p<0.0001 and $F_{2,19}$=7.24, p=0.0046 respectively) but the interaction of GS and patch quality was non-significant ($F_{4,22}$=1.73, p=0.1790). A contrast measuring for differences in
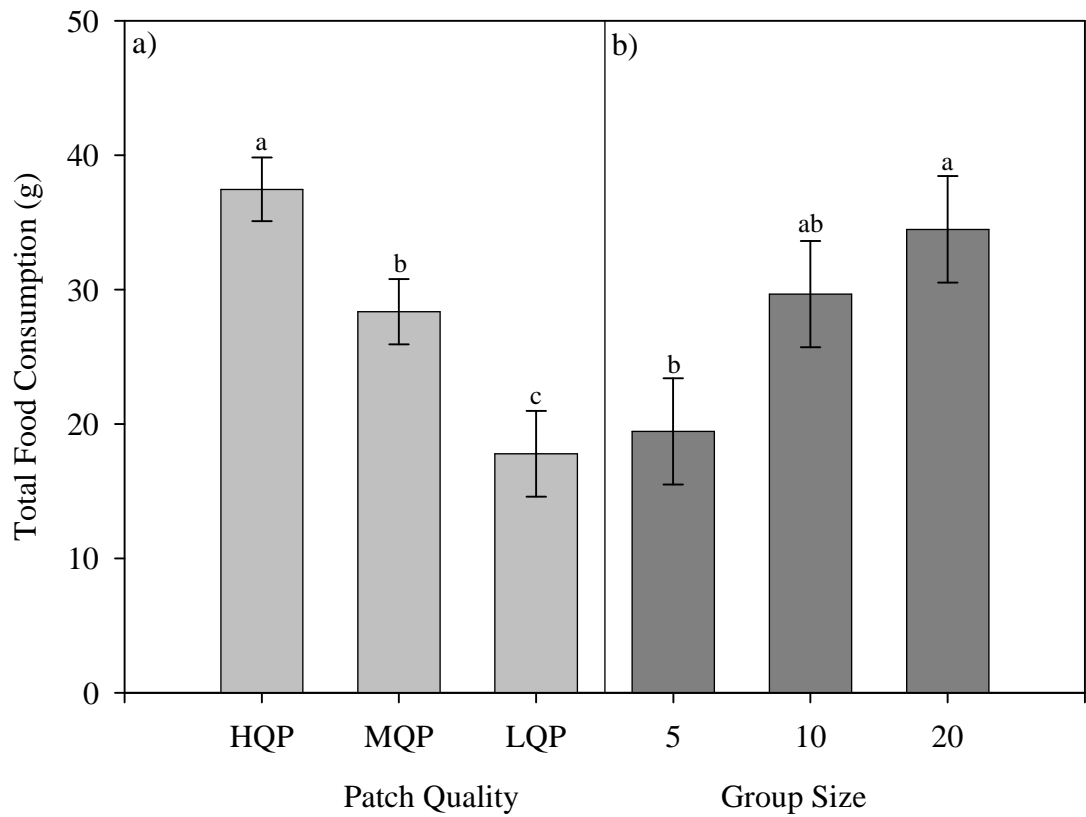
Figure 4-1. Differences in total food consumption at the HQP, MQP and LQP (a) and at GS_5, GS_{10} and GS_{20} (b). Bars represent least squares means ($\pm$ SEM). Bars sharing any identical letters are not significantly different, $p > 0.05$ after Tukey's adjustment.
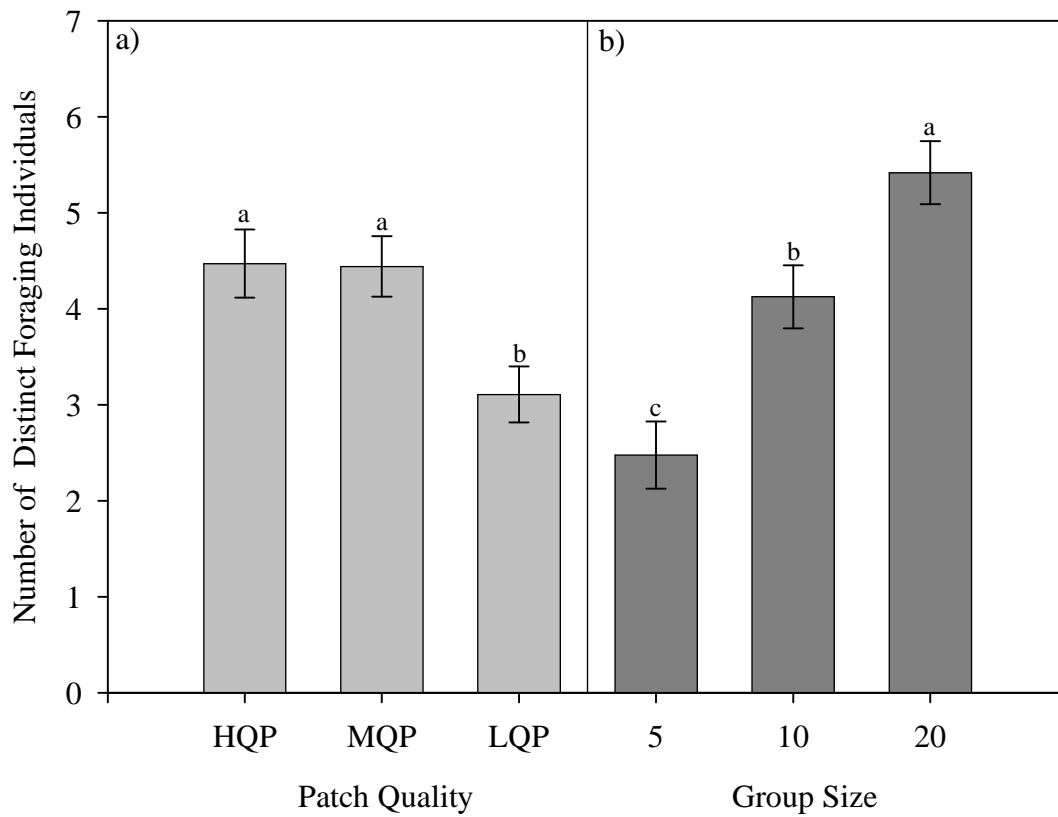
Figure 4-2. The total number of distinct foraging individuals at each patch (a) and in each group size (b). Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05 after Tukey's adjustment.

foraging visits to the LQP and MQP between GS_{10}/GS_{20} and GS_5 demonstrated that on average 2.6 additional individuals visited these lower quality patches at higher GS ($t_{20}=5.15$, $p< 0.0001$). The number of foraging bouts at each patch during the 30 minute testing interval (Fig. 4-3) was significantly affected by GS ($F_{2,21}=4.74$, $p=0.0201$) and patch quality ($F_{2,20}=5.58$, $p=0.0119$) while the interaction effect was found to be non significant ($F_{4,23.2}=0.79$, $p=0.5459$).

Foraging Duration and Patch Residence Time

Two measures of foraging time were calculated, the average foraging duration and the total time a patch was occupied for the 30 minute trial (PRT). Significant effects of GS ($F_{2,12.1}=9.94$, $p=0.0028$) as well as patch quality ($F_{2,13.2}=15.69$, $p=0.0003$) were demonstrated for foraging duration (Fig. 4-4) while the interaction effect was non significant ($F_{4,14.3}=1.96$, $p=0.1564$). Total PRT (Fig. 4-5) was similarly affected by GS ($F_{2,13.2}=13.20$, $p=0.0122$) and patch quality ($F_{2,18.2}=11.86$, $p=0.0005$) but not the interaction of the two ($F_{4,17.4}=0.54$, $p=0.7074$).

Aggressive Interactions at Each Patch

We observed a low overall level of aggression. Therefore for the statistical analysis we used an index of total aggression, combining all behaviors. Despite the overall low frequency of aggressive events we found patch quality to have a significant affect on total aggression ($F_{2,20}=3.68$, $p=0.0436$; Table 4-1) while GS

119
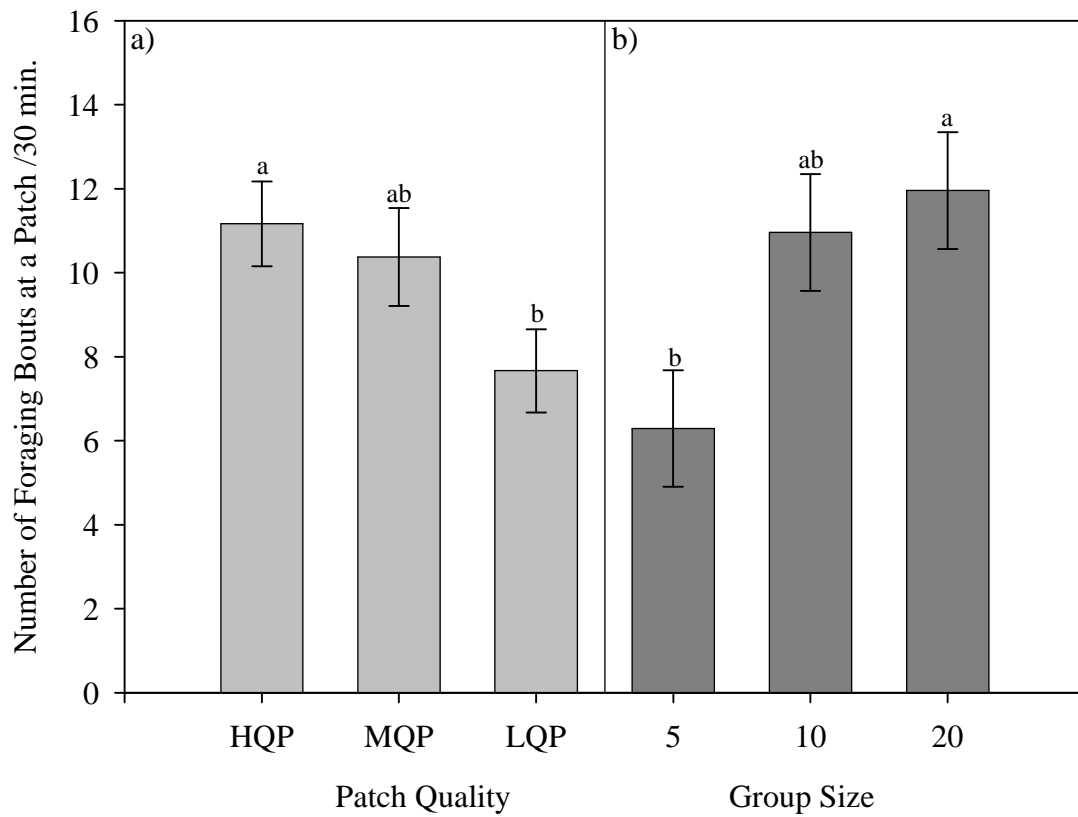
Figure 4-3. The total number of patch foraging bouts per 30 min. testing period, delineated by patch quality (a) and group size (b). Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05 after Tukey's adjustment.
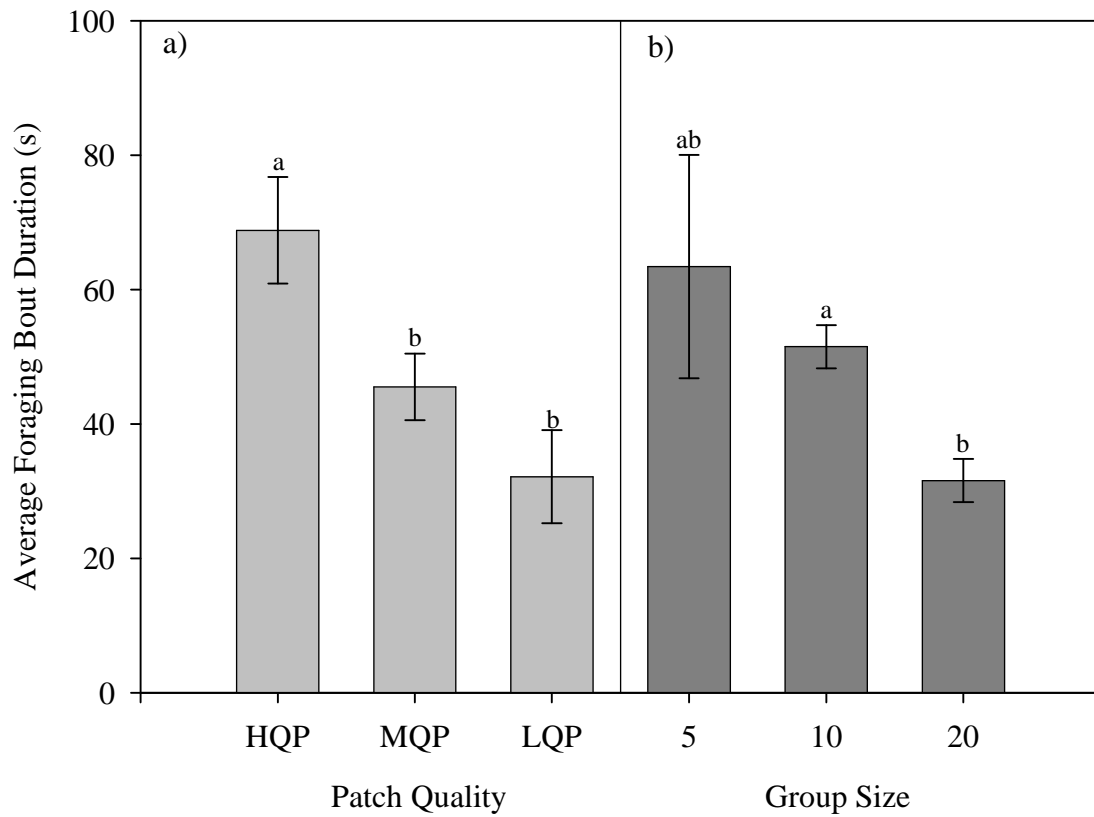
Figure 4-4. Average foraging bout duration by patch quality (a) and group size (b) for the 30 minute testing period. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05 after Tukey's adjustment.
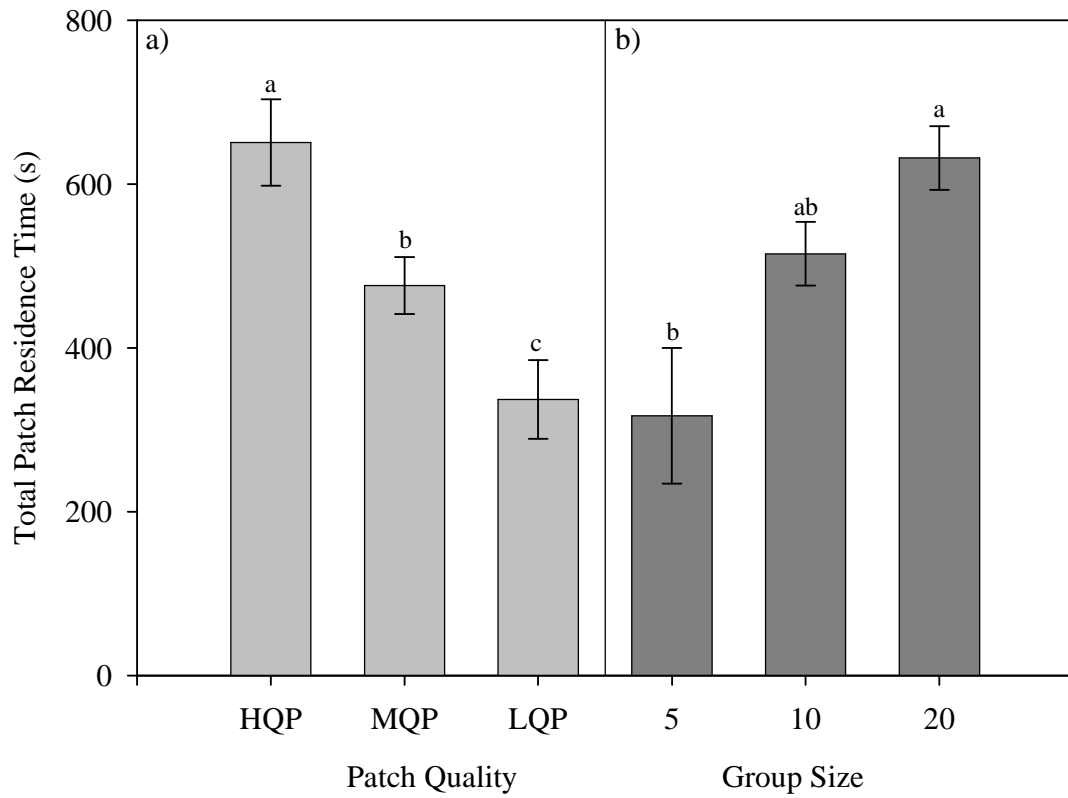
Figure 4-5. Total patch residence time (s) by patch quality (a) and group size (b) for the 30 minute testing period. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05 after Tukey's adjustment.

	Threats	Pecks	Standoffs	Fights	Fights with Pecks	Chases	Total	Total per bird, per trial
HQP	20	26	7	3	2	7	65	0.26 ± 0.08^a
MQP	8	19	4	0	1	5	37	0.16 ± 0.06^b
LQP	4	10	4	0	0	0	18	0.07 ± 0.01^{ab}

Table 4-1. Total number of aggressive behaviors recorded during all testing sessions (n=8), as well as the total number of aggressive interactions per bird, per experimental trial. Only total aggression, measured as a combination of all aggressive interactions, was statistically analyzed (α=0.05). Means $\pm$ SEM are reported, any means with identical letters are not significantly different after a Tukey adjustment.

Figure 4-6. Average number of individuals present at the HQP (a), MQP (b) and LQP (c) at one-minute intervals. Bars represent least squares means (± SEM). Bars sharing any identical letters are not significantly different, p>0.05 after Tukey's adjustment.
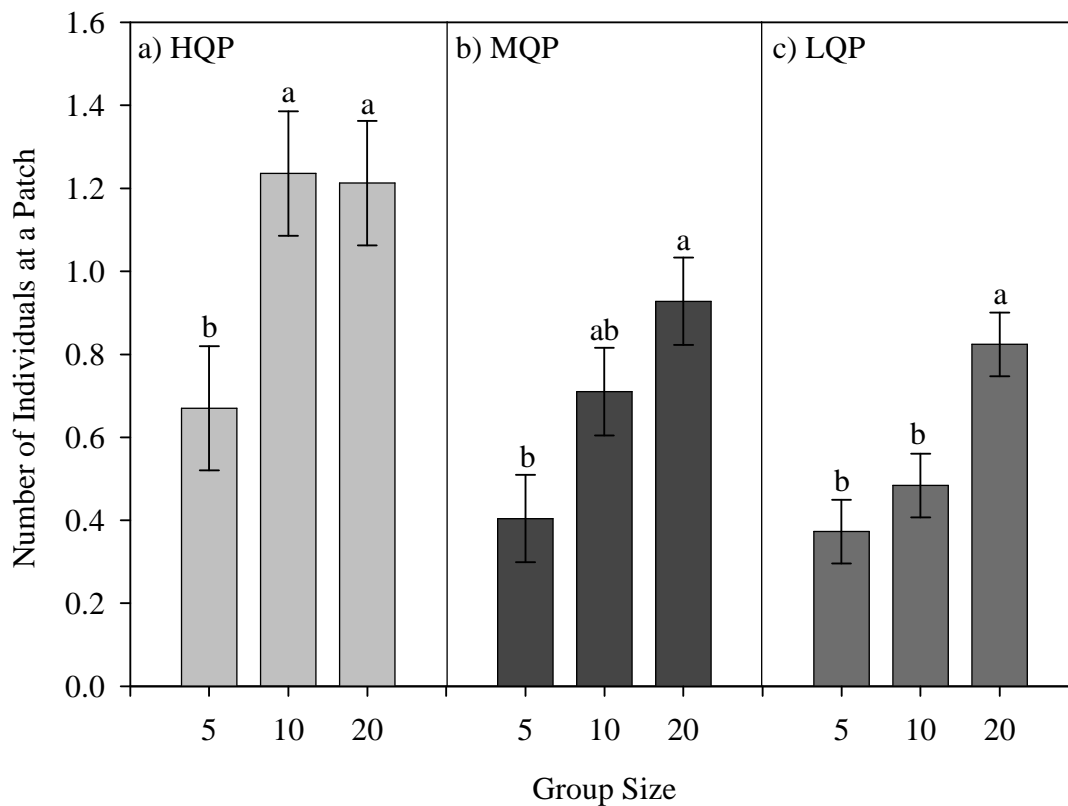
and interaction effects were non significant ($F_{2,21}=0.43$, p=0.6560; $F_{4,23.2}=0.68$, p=0.6122 respectively).

Individuals Present at Patches

Because of the dependence of observations taken at one-minute intervals, time was treated as a repeated measure. For this measurement we were not interested in examining the relationships between patches, but rather the behavior of individuals at each separate patch. Thus the data was separated by patch and each was analyzed separately. There was a significant effect of GS on the number of individuals present at each patch (Fig. 4-6), the HQP ($F_{2,56.2}=4.55$, p=0.0147), the MQP ($F_{2,52.8}=6.24$, p=0.0037) and LQP ($F_{2,50.2}=9.42$, p=0.0003).

Discussion

The results of our investigation demonstrate that despite generations of artificial selection domestic fowl are able to adjust their foraging strategies according to the predictions of optimal foraging theory in order to gain maximum efficiency. Our birds were capable of distinguishing between patches based on the effort required to obtain a food reward and demonstrated a consistent preference for the HQP as opposed to the lower quality patches (MQP and LQP). Because litter was inedible, foraging from the LQP was presumably more labor intensive than doing so from the HQP or MQP. At the HQP we consistently observed a higher number of individuals, a higher number of foraging bouts and increased PRT which all establish the strong preference for this patch.

Birds at all group sizes consumed more food from the HQP, followed by the MQP and lastly the LQP, despite the equal amount of available food at all three patches. As the HQP was depleted its quality diminished relative to the other patches, and birds began exploring other patches. We predicted, and found, an increased usage of the two lower quality patches (MQP & LQP) with GS_{10} and GS_{20} (t=3.07, p=0.0059) because the rate of depletion was greater at these GS as compared to the smaller GS_5. The consumption differences found between patches at each GS corresponded with marginal value theorem predictions, namely that individuals should forage at higher quality patches until that quality equals the average patch quality (Charnov 1976; McNair 1982). Individuals should make use of the best available foraging situation and at large group sizes this entails visiting lower quality patches as a direct result of increased competition due to increased GS.

As predicted the number of foragers, the number of foraging bouts, bout duration and PRT increased with patch quality. In all group sizes birds discerned the superior quality of the HQP, as it required the least amount of work for food, and subsequently visited and foraged from this patch more often than any other. If birds were unable to distinguish patch quality, or showed no preference, then PRT, along with the number of foragers and total foraging bouts should not differ between patches. Despite the scale of patch quality, and without previous experience in this particular situation, birds quickly and consistently distinguished the superiority of the HQP. We expected, however, that if foraging efficiency was improved at the HQP then birds should have spent less time foraging for equal amounts of food from this patch as compared to the lower quality patches.

While sampling is a beneficial and necessary behavior in the wild, its presence in modern domestic species is not required for commercial environments. Animals employing such a strategy will most likely decrease their feeding rate as compared to other, stationary individuals readily feeding. Alternatively, because multiple individuals were foraging from all patches simultaneously the relative quality of the HQP need not necessarily fall below that of the MQP and LQP. At the end of the 30-minute trial an average of 15.5g remained in the HQP while 20.3 and 30.5g remained in the MQP and LQP respectively. Because litter was inedible and presumably remained at each patch the ratio of food to litter remained of better quality at the HQP in relation to the other two, even after extensive depletion.

The results from this study are similar to others that demonstrated the energetically parsimonious foraging strategies of domestic fowl (Schutz et. al. 2001; Andersson et al. 2001; Lindqvist et al. 2002). However this study employed unique approaches because intensely selected animal subject were tested in GS and were not exposed to the experimental treatments prior to data collection. The behavioral responses to patches of different quality were instantaneous rather than conditioned. Birds in this experiment were only acclimated to the transportation, to the testing arena, and the food type. Our experimental animals had no prior information about, nor could they anticipate the availability or varying quality of patches. We examined foraging strategies of the domestic fowl at different GS as opposed to examining strategies of individuals, or testing birds in pairs (Andersson et al. 2001; Lindqvist et al. 2002). It is reasonable to expect that foraging strategies differ when birds are tested in groups versus singly or in pairs (Clark & Mangel 1984).

With only three patches available, each closely situated to the others, it would have been possible for the three most dominant birds to each guard a single patch. Because access was limited to a single bird, only one individual could forage from a patch at any time, while other birds were restricted to either unoccupied patches or 'waiting in line'. If resource monopolization occurred then a maximum of three individuals should gain access to all patches. This behavior was not consistent with our findings at any GS, as on average 4.47 ± 0.355 individuals visited the HQP during the 30-minute testing session. We did not find any evidence in this experiment that birds monopolized patch access at any of the GS. We observed that the number of foraging individuals and foraging bouts increased with GS. These results are contrary to the hypothesis that individuals would defend and monopolize access to resources particularly at large GS as indicated by McBride and Foenander (1962).

The HQP may have become increasingly harder to access at larger GS, due to the increased number of competitors, as there were significantly more individuals foraging from the MQP and LQP in the two larger GS (GS_{20} & GS_{10}) than in the GS_5 ($p < 0.0001$). During testing, when a bird occupied the HQP, subsequent individuals could opt to wait to gain access or forage from the MQP or the LQP. The results suggest that individuals unsuccessful in gaining access to higher quality resources moved on to forage in the lower quality patches. This is a similar finding to those of Estevez et al. (2002), in which domestic fowl were tested in GS of 15 to 120, with patches placed in the centre and periphery of the pen. In both GS the number of birds surrounding a centre patch remained constant but periphery patch visitors increased with GS.

While the number of foraging individuals rose from 3.3 birds in GS_5 to 5.3 birds in GS_{20}, the relative proportion of foraging individuals decreased with GS. The proportion of birds foraging in GS_5 was 65.7% (unique individuals/total number), 48.8% for GS_{10} and 26.3% for GS_{20}. This suggests that a patch may have had a specific saturation point, at which more birds cannot be accommodated. Possibly, the majority of birds from the GS_{10} and GS_{20} were not able to initially gain access to the triangular area where resources were located and thus retreated to other parts of the arena. Rather than expend energy to return and investigate when patches were unoccupied, these birds may have restricted their activities to the other areas of the pen. Broiler fowl often suffer from a high incidence and severity of leg deformities and become increasingly inactive with age (Kestin et al. 1992; Morris 1993; Savory & Mann 1997). These factors most likely contributed significantly to the overall low levels of activity and foraging.

The average foraging duration decreased with increasing GS. This decrease seems to be a byproduct of the increase in the number of foraging individuals. When many birds are scrambling for access, individuals may be able to decrease their exposure to aggression from other group members by decreasing the amount of time spent at a dish. Because individuals from larger GS had potentially more competitors, they may adjust the amount of time spent foraging while others are present. The significantly different number of foraging individuals across GS at each patch supports this notion. Alternatively birds could simply be pushed out of a patch more often in the larger GS, as birds often jostled to gain patch access, and subsequently shortened average PRT for any one individual. This hypothesis of jockeying for a foraging position at the HQP is

supported by the fact that aggression increased with patch quality and the greatest amount was noted at the HQP.

Birds did not change their aggressive strategy in the context of GS but rather according to patch quality. This suggests that birds were operating under optimal foraging theory predictions as they recognized the superior quality of the HQP and thus were willing to expend more energy in order to gain access. Estevez et al. (2002) found an increase in aggression as a function of the number of competitors present, rather than as a function of the total number of individuals in the pen. The fact that aggression did not significantly differ between GS, but did differ significantly with respect to the number of competitors present confirms the hypothesis that it is not the total number of birds present in the pen, but rather the specific number of competitors at a resource, and the quality of that resource, which dictates differences in aggressive behavior (Estevez et. al. 2002). In this experiment birds were most likely squabbling to gain access to resources as opposed to openly fighting to monopolize control of patches.

The definite preference, in all groups, for higher quality patches is well supported by all of the results, including patch consumption, the number of foraging bouts and individual foragers, PRT, foraging duration, the number of individuals present at patches and aggressive interactions. Most likely the non significant patch differences, such as between the HQP and LQP with total aggression, are strictly due to the lack of power. This low level of power is a product of the small sample size available as well as the high variability recorded for some measures. These few non significant results lie in direct contrast to the bulk of the data that is in overwhelming support of distinct behavioral responses to patches of varying quality. Our results demonstrated that, despite

generations of intense artificial selection, in a patchy environment varying along a range of quality, domestic fowl employ strategies that are consistent with the predictions of optimal foraging theory. Birds are not only able to differentiate between sources of food based solely on the amount of work required, but further apply foraging strategies appropriate for the number of competitors present at a resource.

Chapter 5: Summary and Conclusions

Across experiments domestic fowl readily adjusted to the testing conditions and continually behaved according to the predictions of optimal foraging theory. In the cafeteria-style patch discrimination experiment, all measurements taken, patch consumption, number of foraging bouts and individuals, PRT, and aggressive interactions, confirmed that despite generations of artificial selection pressures birds forage optimally in novel and unpredictable environments. Not only have broiler chickens been removed from a natural environment in which foraging strategies shape survival and fecundity, but also the particular birds used in this experiment had no prior experience discerning patch quality. Their immediate and consistent response of choosing the HQP, in all GS, revealed that optimal foraging strategies remain a part of the domestic fowl's behavioral repertoire. The second experiment utilized varying patch locations and sizes and again confirmed the optimal foraging abilities of birds in all GS. Birds adopted non-aggressive strategies when free access was granted to patches, however when access was limited birds scrambled in order to gain, but not necessarily monopolize, patch access.

The use of space by domestic fowl was mostly determined by the size of the testing arena. In the environmental complexity experiment, as well as in the patch location experiment, ICA were not significantly different between GS. Environmental complexity had no effect on ICA, and neither did patch location when access was restricted to a single individual. Neither GS nor environmental conditions affected ICA, suggesting that the testing arena, the only factor constant across GS and experiments, determined how much space individuals utilized. This finding is similar to that of Freed

(2003), who found that the physical amount of space available to birds determined their extent of movement. Other studies as well have shown the determining effects of available space on fowl movement and use of space. Carmichael et al. (1999) found differences in movement patterns across different stocking densities of laying hens, and suggested that crowding effects of increased stocking density reduce the amount of area available to a bird, thus reducing its movements and pen use.

TCA measurements in both the environmental complexity and patch location experiments increased with GS, as were expected. This finding is in accordance with the predictions of behavioral ecology theory; larger GS should take up more pen space and thus the five focal individuals should be more spread apart in these larger groups. Because predation risk is reduced at larger GS (Pulliam 1973) and foraging competition increases (Stahl et al. 2001) we expected larger GS to have larger maximum inter-bird distances in both experiments, which is exactly what we found. The different responses of GS to the experimental conditions were also in accordance with behavioral ecology predictions.

GS_5 was more influenced by environmental conditions than GS_{10} or GS_{20} with respect to environmental patch locations. GS_5 individuals did not benefit from the same level of protection from their small flock size as compared to larger groups, and thus environmental factors should have a greater influence on their behavior. We expected inter-bird distance measures to reflect a higher degree of flock cohesion in this smaller GS, with decreasing flock cohesion as GS increased. This finding was evident in the environmental complexity experiment. However, when tested in the patch location phases, inter-bird distances were more heavily impacted by bird behavior than by GS

133

effects. Behavior appeared to dominate random effect for all of the inter-bird distances, across each experiment. GS_5 was consistently more deviant from randomness than the other two GS, suggesting increased group cohesion at this small GS.

In all experiments aggression was relatively low as compared to other experiments with broiler chickens (Mench 1988; Cornetto et al. 2002; Estevez et al. 2002). Despite the special diet designed to promote health and activity, birds were relatively inactive and non-aggressive (personal observation). This strategy, of little energy expenditure, is most likely highly effective in maximizing growth. In the attempt to increase weight gain and decrease growth time, artificial selection has changed the behaviors of the birds, mainly by increasing feeding motivation and decreasing activity (Katanbaf 1988; Mench & van Tienhoven 1986; Weeks 1994 Jones & Hocking 1999).

When tested in experimental GS different from their home environment individuals changed their behavior, as supported by the consistent GS effects on various behavioral measurements in all experiments. Despite the generations of intense artificial selection for improved performance the behavioral repertoires have not been altered in such a way as to violate theoretical predictions of resource defense, foraging theory, or flocking strategies. These findings have significant implications for production houses and animal management practices. Fowl demonstrated the capacity to respond to environmental conditions not present under agricultural conditions, such as resource patches and changing environmental complexity. Mench (1998) suggested that animals possessing complex natural environments, and demonstrating current behavioral capabilities of adapting and responding to those environments demonstrate a motivation or need for such dynamic environments. In most broiler production houses in the United

States thousands of chickens are kept on uniform, barren litter floors with uniformly and predictably distributed resources. Environments with too little stimulation have been shown to be detrimental to animal health and wellbeing (Wemelsfelder & Birke 1997) just as environments with too much stress and stimulation have been shown to be negative (Rauw et al. 1998). In addition to damaging animal health, stress, boredom, and frustration decrease animal productivity, which is the driving factor for all agricultural systems.

The use of space calculations employed in these experiments, core areas using kernel density estimates, appeared useful as a technique for measuring the use of pen space by confined species. Least squares cross validation was not used in this case, because of the large bias these values produced. Instead fixed kernel smoothing factors of 0.4 were used, after comparisons with 0.8, 0.6, 0.3, and 0.2. While smaller values may have been even less biased, as measured by the amount of core area estimated outside of the pen boundaries, they preserved less information about the shape and general movement patterns of bird core areas. These smaller values produced graphs with small circular areas enclosing individual points where birds were observed. Our experiment demonstrated that core area calculations provide useful information about the use of space of domestic animals, even in confined environments. This technique, in addition with traditional techniques of quadrant analysis can aid in elucidating spacing behavior and patterns of domestic species, despite the difficulties confinement poses to the model.

The behavioral strategies demonstrated by all GS of domestic fowl in each of the experiments conformed to the tenets of behavioral ecology and optimal foraging. Group sizes were differentially affected by environmental conditions, foraged from the highest

quality patch, scrambled for resource access rather wasting energy attempting to monopolize patches, shared resources with conspecifics under free access but fought to gain access when it was limited and maintained inter-bird distances which minimized competition as well as potential predation risk. What is most commanding is that birds had never been exposed to environmental complexity or resource patches prior to the trials; all behavioral responses were immediate and unlearned. Without prior knowledge or experience individuals optimized both the costs and benefits associated with competing behavioral strategies. These optimality decisions are not stimulated in home environments where larger groups have little or no complexity and free access to large, non-depleting resources, thus natural selection has no opportunity to act on the behavioral repertoire of domestic fowl under artificial breeding conditions. The implications of these behavioral responses suggest that domestic fowl are quite capable of complex behavioral responses to environmental conditions. A more complete understanding and manipulation of these behavioral responses can maximize both animal welfare and productivity. Furthermore core area analysis, typically reserved for the study of wild, un-confined species is a useful tool in the investigation of use of space of domestic species.

Appendices

5-1 Testing arena layout for the three treatments. As a control birds were tested in an empty arena without panels. The single treatment consisted of one long pane, represented by the dashed vertical line. For the quadruple panel (quad) treatment four panels were arranged, as designated by the solid lines.

5-2 Expected minimum (a), nearest neighbor (b) and maximum (c) inter-bird distances if birds positioned themselves randomly within the pen space, according to group size (GS).
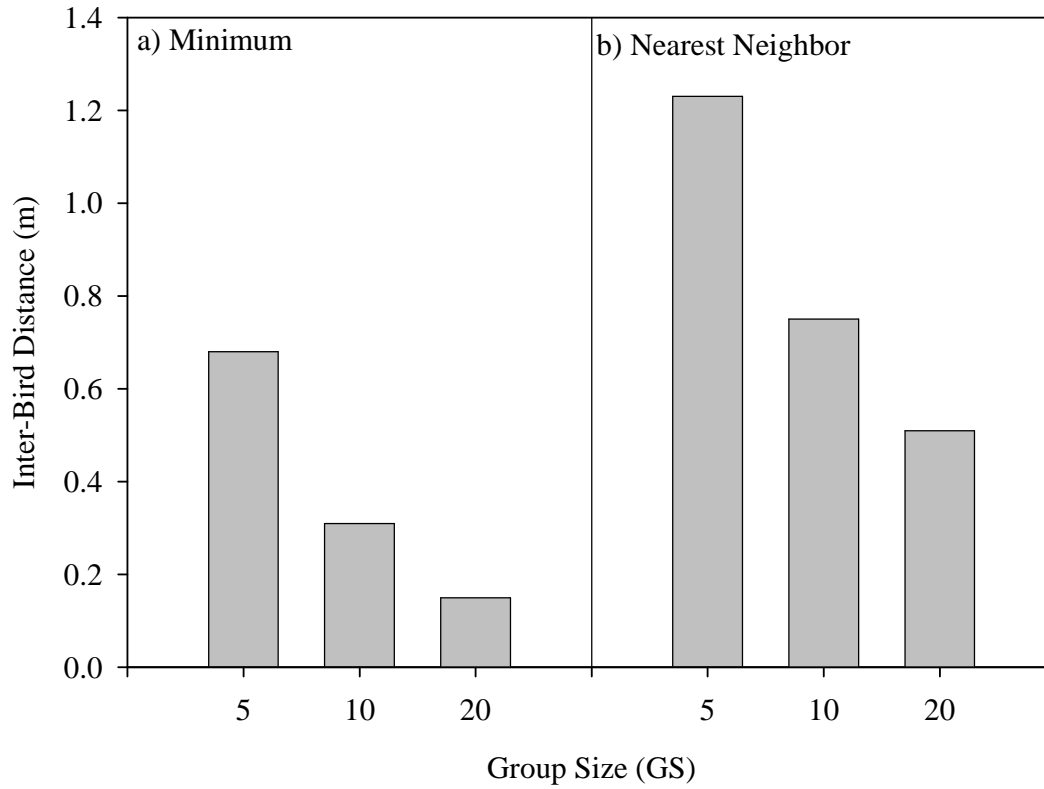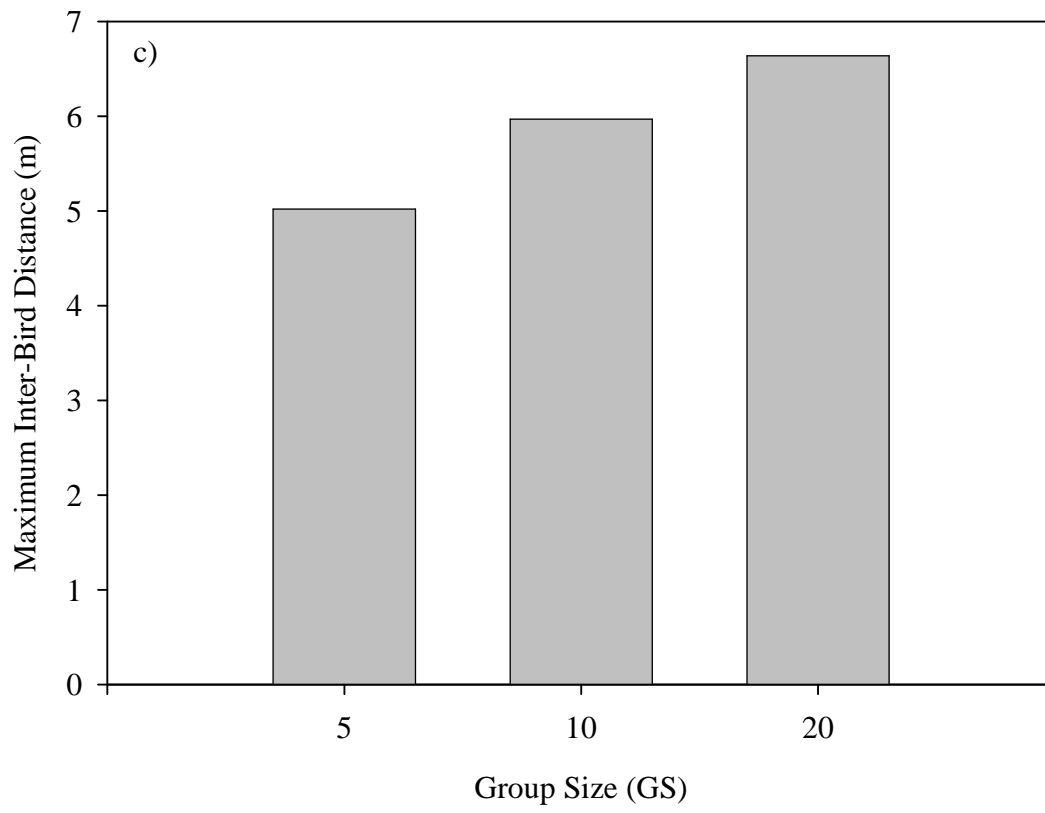
5-3 Distribution of patches in the testing arena. For the clumped treatment one large patch was created in the center, designated by the light grey square with C. For the spread treatment two equally-sized patches were placed equidistance from the center, represented by the two grey squares with S. The patchy treatment consisted of four patches placed along the periphery of the pen, shown by four dark grey squares containing P.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
A																														A
B																														B
C				P																						P				C
D																														D
E								S							C							S								E
F																														F
G				P																						P				G
H																														H
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