Beef feedlot cattle use individual feeding strategies to gain access to feed in a competitive environment

by

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ABSTRACT

Cattle are social animals and frequently interact with other members of their social group, especially when access to food is limited. Despite considerable interest in the social behavior of cattle, no research has focused on assessing the relationship between competition and the feeding behavior of individual feedlot cattle housed in small groups. Forty-five British crossbred feedlot heifers (520.5 ± 32 kg BW) were used to determine how successful competitive interactions impacted an individual's ability to consume and gain access to feed in a competitive feeding environment. Heifers were randomly assigned to 3 pens of 15 animals. Pens were fitted with two radio frequency equipped feed tubs that monitored individual dry matter intake and bunk attendance duration. Cattle were fed a total mixed ration once daily consisting of barley silage, concentrate and mineral supplement at 0900, 1200 and 1500 and had *ad libitum* access to both feed and water. All competitive interactions at and around the feed tubs were monitored continuously from 0900 to 2200 on three separate days. Animals were considered successful if they either gained access to feed, or if they were already eating, they maintained their position. There was a positive relationship between the number of successful interactions displayed and dry matter intake ($R^2 = 0.26$, $P = 0.0003$), bunk attendance duration, ($R^2 = 0.45$, $P < 0.0001$) and bunk attendance frequency ($R^2 = 0.49$, $P < 0.0001$). The strength of these relationships varied dramatically throughout the day and was strongest in the first hour after feed delivery between 0900 and 1000. Large variation between individuals suggests that different animals develop individual feeding strategies in competitive environments. Animals used competition, varied eating rate, and shifted feeding times to access feed. Although this study suggests that the success of an animal in competitive interactions at the feedbunk plays a role in its ability to access and consume feed, individual behavioral differences also play a significant role.

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BW = body weight

DM = dry matter

DMI = dry matter intake

R^2 = coefficient of determination

SCI = successful competitive interaction

SD = standard deviation

SED = standard error of the difference between the means

TMR = total mixed ration

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CO-AUTHORSHIP STATEMENT

Gosia Zobel and Drs. Karen Schwartzkopf-Genswein and Marina von Keyserlingk designed the study collaboratively. Drs. Schwartzkopf-Genswein and von Keyserlingk supervised data collection, analysis as well as manuscript preparation.

CHAPTER 1: INTRODUCTION

Cattle have evolved as herd animals and are naturally social. Unlike feral herds, which consist of a variety of animals of different age and sex, the majority of beef animals destined for slaughter in North America are housed in a "feedlot" in homogenous groups that make social status based on age, size, and sex less obvious. In such conditions, the concept of a true social hierarchy (as seen in matriarchal wild herds of cattle) may not be pertinent. Homogenous groups of cattle may have higher levels of social stress and tension between individuals (Reinhardt and Reinhardt, 1975). This is especially true in common production facilities where many animals are kept together in large feedlot pens; these spatial constraints make it difficult for individual animals to maintain their own personal space, which in turn increases social tension (Kondo et al., 1989).

This review summarizes the literature to date that focuses on the interaction between the social environment and the feeding behavior of cattle housed in commercial feedlots where access to feed is provided via a feed bunk and space per animal is much less compared to that of cattle housed on pasture.

The development of the social environment in the modern feedlot

Although aggressive behaviors are present in even the most resource-abundant circumstances, the number dramatically increases when space constraints are imposed (Craig, 1986; Huzzey et al. 2006). Increased levels of aggression may result in injuries (Leonard et al., 1998), as well as increased susceptibility to disease due to an inability to cope with environmental pressures (Hessing et al., 1995). Further, since animals of similar age, sex and size are normally grouped together, it has been suggested that the negative effects of resource competition may be distributed across the group, and therefore difficult to detect (Stricklin and Kautz-Scanavy, 1984).

Typically, when resources are limited, it is unlikely that access to them will be *proportionally* based on a social or hierarchical rank. Wierenga (1990) demonstrated that social

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rank had limited value in terms of predicting resource access. Moreover, it has been suggested that resource access can be skewed towards one individual. For instance, Blockey (1978) reported that one bull out of a small group (3 or 4 bulls) allotted to a herd of cows would sire 60 to 80% of the calves. Conversely, access to a limited resource by individuals within the group might be skewed so that one section of the group suffers substantially more that the rest of the group. For example, Schake and Riggs (1972) reported that the lower third (in terms of 'rank') of a group of breeding beef cows had access to a disproportionately smaller amount of feed than the remaining two-thirds of the group. This latter example could have detrimental effects on the welfare of certain individuals within the group depending on the extent of deprivation.

Access to resources is dependent on the physical as well as social environment. Not all animals will deal with social and environmental pressures in the same way as their conspecifics when resources become depleted (Benus et al., 1991; Carlstead et al., 1999). It is therefore possible that today's feedlot management practices, which often restrict access to resources such as lying space, shade, water and feed, may impact individual animals differently, and in some cases negatively.

Importance of feeding behavior

Access to feed is one of the most pertinent, and potentially limiting, resources required by feedlot cattle. As calves enter the feedlot, they are typically provided with 30 cm (i.e. Pollreisz et al., 1986) of bunk space per head while they are "backgrounded" and provided rations relatively high in forage. However, as they enter the finishing stage and are provided with high grain diets, feed bunk space is reduced to approximately 20 cm of bunk space per head (i.e. Sowell et al., 1999). As cattle progress through the various feedlot stages the opportunity for all animals to feed at the same time is significantly reduced. Restricted feeding environments have been shown to dramatically increase competition for access to feed and these effects have been shown to be

greatest for 'subordinate' animals (Huzzey et al. 2006). Since research has shown that animals are highly motivated to feed following the delivery of fresh feed (DeVries and von Keyserlingk, 2005), the lack of equal access could have detrimental consequences on certain animals. Animals that are unable to compete may experience delayed eating times (Stricklin and Gonyou, 1981), and may eat more quickly (Olofsson, 1999). Although difficult to quantify, it has been speculated that those animals forced to compete actively for access to the food resource may also expend greater amounts of energy either by displacing other animals or by being frequently displaced by more successful individuals from the feed bunk (McPhee et al., 1964).

General feeding behavior

Feedlot cattle have been reported to synchronize their eating behavior based on sunrise and sunset (Ray and Roubicek, 1971; Gonyou and Stricklin, 1981). Cattle also typically consume their largest portions of feed at sunrise and sunset (Kautz-Scanavy and Stricklin, 1983; Stricklin and Kautz-Scanavy, 1984). As early morning (0100 to 0500) is typically associated with peak rumination in cattle (Wilson and Flynn, 1976) limited eating events have been observed in this period (Gonyou and Stricklin, 1981).

As described above, industry bunk space allotment recommendations for finishing feedlot cattle should be approximately 20 cm per animal; this is low compared to standards for mature dairy cattle (i.e. 47 cm, Longenbach et al., 1999; 60 cm, Grant and Albright, 2001). Furthermore, these industry guidelines may not be followed, as indicated by increasing research demonstrating the potential benefits of reduced bunk space. For instance, Zinn (1989) showed that limit-fed feedlot cattle provided with 15 cm of bunk space could maintain 1.45 kg d^{-1} gain. Gunter et al. (1996) indicated that 12.7 cm was sufficient to maintain gains of 1.07 kg d^{-1}. Unfortunately these studies focused entirely on productivity measures, and did not consider behavioral and social

impacts of such space allotments. Further work should consider the impacts of extremely competitive environments on individual animals.

It has been suggested that individual animals with reduced or sub-optimal access to feed may face health and performance repercussions (Fraser and Broom, 1997). Altered feeding behavior such as feeding at night (Stricklin and Gonyou, 1981; Swanson and Stricklin, 1985) or high rates of consumption (Kenwright and Forbes, 1993) triggered by competition for access to the feed bunk, could have detrimental consequences on the welfare of individuals. For instance, it is becoming increasingly recognized that morbid feedlot cattle have altered feeding behavior patterns compared to healthy feedlot cattle (Sowell et al., 1999; Schwartzkopf-Genswein et al., 2004). It has also been suggested that animals with higher eating rates may also be more prone to increased ruminal NH_3 concentrations (Montgomery et al., 2004), indicative of unstable ruminal environments that may lead to acute or sub-acute rumen acidosis (Stricklin, 1986; Montgomery et al., 2004). Rumen acidosis is a concern in terms of productivity losses for the producers (Gibb et al., 1998; Schwartzkopf-Genswein, et al., 2003) as well as having negative welfare implications for the animals, such as sudden death (Glock and DeGroot, 1998).

Social organization

In order to assess how individual animals access feed in a feedlot environment where access to feed is often limited, it is important to understand the social organization of a group of cattle. Despite the study of social behavior in livestock having its beginnings in the early parts of the 20th century, the concept of hierarchical orders as outlined in the literature today evolved over a number of decades. The initial research focused on describing the social environment of chickens (Schjelderup-Ebbe, 1922), sheep and goats (Scott, 1942), and deer (Darling, 1937). The concept of hierarchical orders and dominance relationships surfaced in the work of Woodbury (1941), who referred to some animals being superior to others because of their horns or bunting abilities.

In the mid-1940s, Guhl and Atkeson (1959) investigated how physical and physiological factors affect relationships in cattle. Schein and Fohrman (1955) introduced the study of hierarchical relationships in cattle when they published a detailed examination of aggressive behaviors and their impact on herd dynamics. Unlike many of today's studies of social organization in cattle, their work took into account indirect aggressions such as approaches and threats as well as obvious physical acts. Although their work was descriptive in nature, these authors claimed that the concept of dominance should be based on all competitive behaviors, and not just those arising from physical contact. Although the cattle observed in the Schein and Fohrman (1955) study were observed primarily in a pasture setting, these authors do make reference to a dry lot situation in which some cows were able to control the food resource (piles of hay) better than others. In this latter case, certain individuals were noted to spend a great deal of time attempting to gain access to feed. Schein and Fohrman (1955) used this disparity in hay access as evidence to state that, "there is little doubt that the lower order animal would suffer markedly if she were wholly dependant on trough feeding". It is interesting to consider that over half a century ago, researchers were already noting the implications of resource-limited environments. Today's beef feedlot management practices exemplify similar types of circumstances that these scientists in the mid 1950s considered detrimental to the welfare of some individuals within a group. Although the importance of their statement has been lost in many of today's social organization studies, Schein and Fohrman's thoughts lend well to the idea that current management practices likely do impact the welfare of cattle.

The welfare of cattle has often been assessed in terms of easily quantifiable factors, such as productivity and health. For instance, aggressive behaviors have been used to establish dominance hierarchies, which are then related to a measure of productivity such a milk yield (Beilharz et al., 1966; Soffié et al., 1975). Although this performance measure may be indicative of poor welfare in some cases (i.e. Milne et al., 2003), milk yield is not generally recommended as a valuable

measure of welfare status because of confounding genetic and environmental factors (Main et al., 2003; Whay et al., 2003). Generally, the best indicators of welfare include physiological and behavioral measures (Broom, 1991). As such, the results of studies comparing only performance-related measures to dominance status as an indictor of welfare status of animals within a group should be used with caution. Broom (1988) also cautions that animals develop various coping mechanisms in stressful situations, and so some indictors may be more useful for certain animals over others.

Only a few studies have assessed general health impacts of social hierarchies in beef cattle (i.e. Stricklin and Gonyou, 1981; Mench et al., 1990). To the best of my knowledge, no study has attempted outward quantification of the welfare status of beef cattle using the concepts of dominance or social hierarchies.

Determining social organization in cattle using the concept of dominance

Spatial constraints in most feedlot situations mandate that cattle interact substantially more than they would on pasture (Orihuela and Galina, 1997). These interactions occur in various ways, and differ according to the environmental and managerial situations. Upon mixing and new introduction of individuals into a group, initial interactions are often physically aggressive, and then regress to non-contact approaches within days of mixing (Tennessen et al., 1985). Not surprisingly, owing likely to their ease of observation, obvious physical interactions were very quickly chosen as a means for assessing the social structure of a group of cattle (i.e. Stricklin, et al., 1979; Mendl et al., 1992; DeVries et al., 2004). A common method of determining social order is via dyadic relationships based on the outcomes of competitive interactions between pairs of animals (observable behaviors such as displacements of one cow by another at a resource). This method is typically used to determine the dominance level (i.e. dominance index; Mendl et al., 1992) or the aggressiveness level of animals (i.e. aggressiveness index; Tilson et al., 1988). Each

incident of competitive behavior is assessed in simple terms based on a physical interaction; namely, identifying which animal was the instigator (the individual that directs an action towards another individual) and which was the reactor (the individual that responds to the action by the instigator). The instigator is then classified as being higher ranked than the reactor. The dominance index takes into account the number of animals dominated, whereas the aggressiveness index considers all competitive incidences. These are then combined into a matrix and extrapolated to develop a general competitive order of the individuals in the group.

Alternatively, other researchers have attempted to capture a more complex social environment by taking into account supplementary behavioral observations during each of the competitive interactions used to assign social orders. For instance, using the original work of Schein and Fohrman (1955) and the definitions of Dickson et al. (1967), Stricklin et al. (1979) developed four classes of behavioral interactions ranging from those with most contact (such as a fight or bunt) to those with no contact (such as head thrusts and avoidance). A fight was defined as reciprocal aggression between two animals and a bunt referred to un-reciprocated contact between one animal and another. The non-contact interactions were either head thrusts (where an attack movement is made but not carried through), or avoidance (where an animal responds to the presence of another by moving away). Olofsson (1999) used similar definitions to those described by Stricklin et al. (1979), but referred to bunting under the category of pushing and butting. Furthermore, Kondo et al. (1989) distinguished between the actions that could arise within a bunt (splitting the category into a bunt and a push). In another approach, Barroso et al. (2000) split the behaviors into two different categories: "active" and "non-active" dominance. Active dominance referred to threats (such as previously termed 'head thrusts') and aggression (referring to any direct contact, from a mild bunt to a severe fight). Non-active dominance referred to retreat (such as avoidance), supplant (animal takes away another's resources) and displacement (one animal walks towards another until it retreats).

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Nonetheless, even with the incorporation of more detailed observations described above, animals were ultimately categorically ranked, and the individual differences between animals were not considered. Although the definitions for, and categories of, dominance interactions have progressively become more detailed, there remains a lack of focus on the individual animal; namely, without exception, the aforementioned definitions of dominance fail to properly incorporate individual differences in behavior.

From a statistical standpoint, placing animals into categories (i.e. 'dominant' and 'subordinate') or giving them ordinal ranks relative to one another is advantageous. Unfortunately, the lack of linearity in many groups challenges the feasibility of using such measures of status as dependent or independent variables (Rushen, 1984). Nonetheless, Rutter et al. (1987) made an important observation that cattle do not know (nor would they likely care if they did know) their "rank" in a group's hierarchy. Arave et al. (1984) suggested that under common management practices, the assignment of dominance values might be inconsequential in studies of the social environment. Commonly utilized dominance indices are as much a function of the artificial space allowances and other limited resources in commercial feedlots as they are a function of the aggressive interactions used to calculate them.

The results produced by various ranking methods are not always analogous to one another and comparisons between methodologies on the same data sets have resulted in at best weak correlations between the ways animals are ranked (Tennessen and Gonyou, 1981; Val-Laillet et al., in press). In addition, the ranks established at different resources (i.e. feed versus resting areas) do not necessarily correspond with one another (Lobato and Beilharz, 1979; Phillips, 1993). For example, Soffié et al. (1976) noted that the dominance order based on access to feed was not correlated to the order based on access to the milking parlor in dairy cows. Thus, caution is warranted when access to a particular resource based on social rank is assessed, as animals within a group may not value resources equally.

Considerable research to date has assessed social hierarchy based on displacements at the feed bunk; not only does this assume a direct link between competitive vigour and successful access to a resource, it also makes conclusions difficult to interpret. For example, Huzzey et al. (2006) suggested that 'subordinate' cattle were frequently displaced at the feedbunk in highly competitive environments (Huzzey et al. 2006). However in this previous study, displacements from the feedbunk was the only criterion used to determine dominance categories. Clearly, if Huzzey et al. (2006) had used an alternative dominance classification system that did not consider displacements, the conclusion that certain animals display specific feeding behaviors compared to others would almost certainly be different. Therefore, even when definite conclusive statements are possible, they must be interpreted in context of their methodology.

The lack of agreement between schemes that rely on dominance and hierarchical orders suggest that actual social organization in group-housed cattle may not be as well defined as the scientific community believes. Rather than focusing on categorizing individuals within a group, it may be more useful to consider the physical and social responses of individual animals to their social environment and compare how these responses relate to morbidity or performance.

Alternative means of assessing social organization

In 1981, Reinhardt and Reinhardt asserted that research based on the notion of dominance, rank and hierarchical orders has taken precedence over research investigating the presence of other relationships (e.g. amicable) between cattle. Considering subtle interactions, such as allogrooming, may illustrate a more accurate representation of the social organization within groups of cattle (Rowell, 1966; Fraser and Broom, 1997). Further, some animals (often those classified as lower ranked) have been referred to as 'peacekeepers' of a group, exhibiting subtle reaction-based behaviors such as tolerance and avoidance (Fraser and Broom, 1997). Kondo and Hurnik (1990) suggested that something as simple as a change in posture of one animal might be an effective

discriminative cue for another individual to avoid a potentially aggressive situation. Some animals make more effort in maintaining space relative to others (Beilharz and Zeeb, 1982), while others actively avoid specific animals, even when these (presumably more 'dominant') animals make no overt acknowledgement of the others' presence (Rowell, 1974). This may be because of individual animals possessing unique sensory cues, sometimes referred to as a 'signature system' (Beecher, 1989). These cues may develop as familiarization with individuals in the group occurs. Repeated encounters establish an individual recognition of each group member, based on the different observed cues (Stookey and Gonyou, 1998; Kristensen et al., 2001).

In addition to avoidance behaviors, animals in groups have also been known to form alliances (i.e. Rowell, 1974; Bernstein, 1981). Although minimal work has been done on social alliances in livestock, a few studies confirm the existence of relationships where individuals may benefit from the presence of a superior (Tyler, 1972; Swanson and Stricklin, 1985) or where both individuals benefit by cooperatively eating and preventing others from displacing them (Stricklin and Gonyou, 1981). Although the specific mechanism behind the development of aggressive versus passive and even amicable behaviors in feedlot cattle is uncertain, it is important to recognize that avoidance and partnership behaviors contribute to the social stability of a group.

It is not possible to assess all interactions and subtle behaviors when examining group dynamics; however, by keeping in mind that other less obvious competitive interactions happen at a resource, an observer will be able to draw better conclusions about the individual behavioral differences in each individual.

Individual differences in behavior

Since the late 1970s and early 1980s, behavioral ecologists have been describing differences in behavior between individuals in a group (i.e. Henry, 1977; Milinski and Parker, 1981); this research later spurred the notion of quantifying individual differences in behavior

(Wilson et al., 1994; Coleman and Wilson 1998). Some of the more detailed research focused on coping styles for dealing with stress and resource depletion (Benus et al., 1991). Carlstead et al. (1999) stated that the development of individual coping mechanisms is largely based on individual characteristics, as well as past experience when dealing with situations. Broom (1991) indicated that an animal's ability to cope with its environment was a direct indicator of its welfare, whereas inability or difficulty in coping with environmental stressors indicated poor welfare.

Good health is an important component of welfare, and numerous studies have shown that an individual's health will suffer when it is unable to cope with an environmental stressor (i.e. Olff et al., 1993; Hessing et al., 1995). Recent work has indicated that feeding behavior, in particular, is predictive of health disorders in beef cattle (Quimby et al., 2001; Sowell et al., 1999). In other work on dairy cattle, Huzzey et al. (2007) showed that cows that were less likely to approach the feed bunk, ate less, and were more likely to get sick. It is therefore important to recognize the different ways in which individuals attempt to cope with resource-limited situations in order to insure good health and welfare.

A coping style is a consistent set of behavioral and physiological responses of an individual animal to stressful environments (Koolhaas et al., 1999). Benus et al. (1991) described two different, but equivalent, coping styles used by rodents faced with an aversive situation. In a social setting, some individuals developed active or aggressive responses, while other individuals adopted a passive approach. Although most work on individual differences in coping strategies has focused on rodents and wildlife, research with pigs (Spoolder et al., 1996) and cattle (Hopster, 1998) has indicated that many behavioral responses to specific stressors remain relatively stable over time. This indicates development of distinct coping styles by individuals. Although not specifically measuring individual differences in behavior, Syme et al. (1974) found that some animals were more 'skilled' than others at obtaining resources, and Sherwin (1990) found that even in cases where trough space was not limited, some steers simply butted more than others. Of course, some

individual differences will always be present because the motivational drive for animals to behave in certain ways changes based on temporal and environmental factors. For instance, an animal that is not necessarily a good competitor may still gain access to feed when it is exceptionally motivated in doing so, such as during the initial morning feed delivery (Arnold and Maller, 1974; DeVries and von Keyserlingk, 2005). Therefore, in order to identify individual differences in behavior of cattle, it is important to consider the motivational state of the individual.

<u>Importance of measuring individual differences in behavior</u>

The precedent of ranking animals and establishing hierarchical orders has made the scientific community lose sight of establishing a simple means to assess how modern production practices actually affect individual animals by altering their social behavior. Stricklin and Kautz-Scanavy (1984) suggested that assessing cattle as a group rather than individually may mask the impact of social stress on production outcomes. The drawbacks of assessing cattle as a whole group were demonstrated by Larson et al. (1992) who showed that averaging individual feed intakes reduced variation by as much as 10 times, as well as eliminating treatment differences. Thus, identifying the different ways in which individuals react to the stress of limited resources may provide insights about how our current production practices impact the individual.

Objective

The study described in Chapter 2 of this thesis focuses on identifying the effects of competition on access to one primary resource – feed. The means by which competition was assessed is crucial in understanding the marked difference of this study from those previous to it. In an effort to observe the subtleties of group dynamics, competition was a function of direct and indirect displacements. Even more importantly, non-instigating animals that defended and maintained their position at the feedbunk were also noted as being competitively successful. Finally, the final count of successful competitive interactions was not manipulated into a social

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rank order, nor were animals assigned dominance status. This allowed for the comparison of each individual's highly variable competitive behavior across the day to its equally variable feeding behavior.

Hypothesis

It was hypothesized that in a competitive feeding environment, competitively successful animals would have greater dry matter intake, fewer but longer visits, and slower eating rate than their less competitively successful counterparts. In addition, my aim was to demonstrate that individuals differed from one another in terms of their feeding strategies when attempting to gain access to feed.

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CHAPTER 2: BEEF FEEDLOT CATTLE USE INDIVIDUAL FEEDING STRATEGIES TO GAIN ACCESS TO FEED IN A COMPETITIVE ENVIRONMENT[1]

Introduction

Understanding the impact of social interactions on feeding behavior may provide insight into the welfare and production of feedlot cattle. The social behavior of cattle is typically associated with dominance hierarchies determined using mathematical computations including dominance indices (e.g. Boyd and Silk, 1983) and agonistic indices (Schrader, 2002) and assigning a rank order to individuals based on observed wins and losses. Arave et al. (1984) questioned the assignment of dominance values when studying the social environment of cattle housed intensively, particularly when space is limited but feed supply is constant. Subordinately classified animals may be simply adjusting their behavior to avoid agonistic interactions in order to gain access to resources (Arave et al., 1984). Further, some studies have suggested that aggressiveness does not directly reflect dominance (i.e. Stricklin and Gonyou, 1981; Beilharz and Zeeb, 1982), indicating that more than just successful aggressive interactions should be considered when comparing the social behavior of intensively housed cattle. This can be achieved in part by considering instances where animals successfully defend their access at the feedbunk, oftentimes by not using physical retaliation. In other words, a reactor, rather than an instigator, maintains its space at the feeder and no displacement occurs. Therefore, in addition to successful aggressive interactions commonly used in dominance indices, considering non-physical displacements as well as non-instigated feedbunk defence behaviors may provide a more accurate representation of how competition impacts resource access by an individual.

Although it has been suggested that a more comprehensive assessment of social behavior is needed for comparing individuals within groups, little research to date has done so in intensively

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[1] A version of this chapter has been submitted for publication.

housed feedlot cattle. It was not, however, the purpose of this paper to compare previously used dominance indices with a more comprehensive assessment. Rather, the objective of this study was to produce hourly counts of successful competitive interactions for each individual animal and then determine the relationship between these counts and the individual animal's ability to consume and gain access to feed in groups of recently mixed feedlot heifers fed in a competitive feeding environment. The impact of differences in individual behavior patterns on access to feed was examined and discussed.

Materials and Methods

Animals

Forty-five crossbred heifers (520.5 ± 32 kg BW), were blocked by BW and assigned to 3 groups of 15 animals. Each heifer was tagged with a radio frequency (RF) transponder 6 cm from the base of their right ear (Allflex USA Inc., Dallas/ Ft. Worth, TX 75261-2266). The transponders were required for the collection of feeding behavior data using an electronic feed bunk monitoring system (GrowSafe Systems Ltd Airdrie, Alberta). All heifers were cared for according to guidelines of the Canadian Council on Animal Care (CCAC, 1993). The experiment took place during July of 2004.

Housing, feeding and daily routine

The heifers were housed at the Agriculture and Agri-Food Research Centre in Lethbridge, Alberta in pens measuring 40.2 m × 27.4 m with a centrally located water system (Bolhmann Inc., Denison, IA) and a 2.4 m × 24.5 m concrete apron directly in front of the feed tubs. Each pen contained two feed intake tubs measuring 0.91 m 0.38 m × 0.53 m (approximately 0.5 m of the width was accessible for feeding, giving approximately 7 cm of bunk space per animal). Animals were fed a balanced maintenance diet consisting of 40% barley, 3% supplement, and 57% barley silage on a dry matter (DM) basis according to NRC (2000) guidelines, allotted equally across

three daily feedings at 0900, 1200 and 1500 to accommodate *ad libitum* appetite. Orts were removed daily, and pooled feed samples, taken from each tub at the beginning and end of the trial, were frozen for DM analysis. Fresh water was available at all times. Straw was used for bedding and was placed in the pens as needed.

Feeding behavior

GrowSafe System. Pens were equipped with an electronic feed monitoring system using radio frequency technology capable of monitoring individual intake and feed bunk attendance patterns of all cattle within the pens 24 h per d (GrowSafe Systems Ltd Airdrie, Alberta). The system consisted of 2 individual feed tubs each measuring 0.38 m × 0.53 m × 0.91 m and placed on 2 load cells. The rim of the tub was fitted with an antenna that radiated a 134.2 kHz electromagnetic field. The antenna was designed to receive an electromagnetic signal from the ear transponders when they were within approximately 50 cm of the each other. Energy produced by the antenna was collected by the transponder, which then transmitted an electronic identification (EID) number back to the antenna. A reader panel differentiated between individual transponders and stored data every 2 s onto a desktop computer. The computer, connected to the reader panels with a data cable, was housed in a building immediately adjacent to the pens. Scale readings (kg) from each feed tub were also transmitted every 6 s with the same data cable to the computer using data acquisition and analysis software (GrowSafe Vers. DAQ 4000E). For a detailed description of this system please see Wang et al. (2006).

Feeding Behavior. Dry matter intake for each individual animal was summarized as kg of intake per h. DM content of feed was established by drying samples at 55 °C in a forced-air oven for 72 h, ground, and passed through a 1-mm screen. Bunk attendance (BA) duration was summarized as the time the animal had its head down in the feed tub (min h^{-1} per animal). BA duration and DMI values were used to calculate eating rate (kg min^{-1} h^{-1} per animal). BA frequency

was summarized by hour. A new BA frequency count was recorded each time GrowSafe registered that an animal returned to the feed tub, regardless of time since the last visit.

<u>Competitive behaviors</u>

Animal Identification. A 50-mm paint brush was used to apply a 45-cm ID letter using sheep branding paint (Si-Ro-Mark, Australia) to the back of each animal approximately 10 cm behind the shoulder. Twenty-four hours later, a coat of latex exterior flat paint was applied over the branding paint (white for dark colored animals and black for light colored animals).

Recording. Each feedlot pen was also equipped with a video surveillance system, consisting of a digital video camera (Panasonic WV-CP474; Mississauga, ON, Canada) fitted with a varifocal lens (Tamaron 13VG2812AS 2.8-12mm; Saitama-City, Japan) encased in an environmental housing (Pelco EH3512-2HD/MT; Clovis, USA). Cameras were mounted on metal posts 4.9 m directly above the feed tubs. Video was captured using Omnicast, Genetec (Dorval, Quebec) software and stored on a PC until it could be converted to AVI files for viewing in Observer (Noldus, The Netherlands). Competitive interactions between animals were recorded when displayed within an approximate area of 8.4 m^2 (Figure 2.1) from 0900 to 2200 for 3 non-consecutive days (d 1, d 3 and d 7). The animals were mixed into new groups on d 1 at 0830 and recordings began at 0900, upon feed delivery.

Coding. Much of the previous work on the social behavior of cattle fed in a competitive environment has focused exclusively on successful displacements from the feeding area as an indication of the social dominance between animals (Huzzey et al., 2006). Although the authors argue that the use of such interactions aids in inter- and intra-observer reliability, it can exclude non-physical interactions between individuals. As such, the definitions used to code competitive behaviors at the feed tubs in this study (Table 2.1) took into account the instigator's competitive physical and non-contact interactions, as well as the outcome of the interaction. Both the instigator

and the reactor were noted. If the instigator successfully gained access to one or both feed tubs, it was considered competitively successful. If an instigator was unable to displace a reactor, the reactor was coded as having been successful. Behavior variables were left as counts; they were not used to calculate sociometric measures such as those used by Lamprecht (1986) and Kondo and Hurnik (1990). For comparison purposes, competitive success was considered to be similar, but not equal to, dominance.

Intra- and Inter-Observer Reliability. Percent agreement does not take into account that agreements may be solely based on chance (Hunt, 1986). Therefore, we used Cohen's kappa coefficient (Cohen, 1960) to evaluate intra- and inter-observer reliability. Inter-observer reliability was found by comparing the behavioral codings from two observers for two 20-min periods ($\varkappa$ = 0.78). Intra-observer reliability was evaluated by having one of the observers code behaviors in two 20-min periods on two different days ($\varkappa$ = 0.85). All video recordings of behavior were coded by one observer following establishment of intra-and inter-observer reliability scores.

Statistical analyses

Feeding behavior data collected on occasions when the electronic monitoring system failed to function because of power failure, mechanical problems, or failure of a main computer board (1 to 2% per test) were excluded from all subsequent analyses. The final data set consisted of dry matter intake (DMI; kg h^{-1}), eating rate (rate; kg min^{-1} h^{-1}), bunk attendance duration (BA duration; min h^{-1}), frequency of bunk attendance (BA frequency; visits h^{-1}), and a count of successful competitive interaction (SCI; count animal h^{-1}) for h 0900 to 2200 on each of the 3 d. Descriptive statistics were calculated using averaged daily data for each animal (for daily values) and averaged hourly data for each animal (hourly values).

The relationships between SCI and each feeding behavior variable (DMI, rate, BA duration and BA frequency) were established by the following steps using SAS software (SAS Institute,

1999). Data were first summarized by animal and were screened for normality using Proc Univariate in SAS. Proc Mixed in SAS was then used to create separate models for each variable for the analysis of covariance (separate regression lines fitted for each pen). The univariate procedure was then used on the residuals of each model in order to identify and remove extreme outliers. Once outliers were removed, basic descriptive statistics were found with the univariate procedure. Proc GLM was used to establish the R-squared values for each model. A similar procedure was followed for determining hourly and individual animal relationships between SCI and each feeding behavior variable, with the following three exceptions: First, data were summarized by hour and animal. Second, data were analyzed separately by hour and by individual animal (i.e. included as by statements in the Proc Mixed and Proc GLM analysis). Lastly, within the hourly analysis, separate models were applied to each hour.

In order to put the highly variable and individual relationships into perspective, R^2 values were categorized in the following way: weak relationship (R^2 values between 0.2 and 0.4), moderate relationship (R^2 values between 0.4 and 0.6) and strong relationship (R^2 values above 0.6). When relationships between variables were reported for individual animals, the R^2 value was used a descriptive value.

Results

Descriptive statistics

Table 2.2 provides descriptive statistics for DMI, eating rate, BA duration, and BA frequency, as well as SCI by day and by hour. Variation was great for all variables except DMI. Eating rates ranged from 92 g min^{-1} to almost 500 g min^{-1}. Similarly, feeding times ranged from just over 20 min to almost 2 h daily, and as little as one minute to as much as 8 minutes in an hour. The frequency at which animals visited the bunk also varied greatly, both daily and hourly.

Animals were involved in a minimum of 35 SCI per d (2.7 per h), but some animals maintained more than 5 times as many SCI. No relationship was found between animal weight (kg) and SCI ($R^2 = 0.038$, $P = 0.20$).

Relationship between successful competitive interactions and feeding behavior

DMI. A weak positive relationship was evident between DMI and SCI ($R^2 = 0.26$, $P < 0.0003$). On an hourly basis, the strength of the relationship varied across the day (Figure 2.2). The relationship was strongest between 0900 and 1000 (the hour after morning feed delivery) ($R^2 = 0.77$, $P < 0.0001$). After this period, the relationship generally declined, culminating with the weakest R^2 value 2 h following the midday feed delivery between 1400 and 1500 ($R^2 = 0.22$, $P = 0.01$). The relationship between SCI and DMI increased 1 h after the last feed delivery ($R^2 = 0.52$, $P < 0.0001$). The relationship weakened in early evening, but then increased. The final relationship was moderate and was observed between 2100 and 2200 ($R^2 = 0.55$, $P < 0.0001$).

The relationship between DMI and SCI was highly variable between individuals, ranging from an $R^2 = 0.27$ to $R^2 = 0.92$. Figure 2.3a illustrates that 56% of the heifers in this trial exhibited strong ($R^2 > 0.6$) relationships between their DMI and SCI. In contrast, only 18% of the heifers had weak ($R^2 < 0.4$) relationships between their DMI and SCI. The remaining 27% of the heifers exhibited moderate relationships ($R^2 = 0.4$ to $R^2 = 0.59$) between DMI and SCI.

Eating Rate. There was a weak positive relationship ($R^2 = 0.18$, $P = 0.005$) between eating rate and SCI, but no hourly relationships were observed. On an individual basis, the eating rate of most heifers was not affected by their SCI; however, 16% of the animals did exhibit weak to strong relationships between eating rate and SCI ($R^2 = 0.23$ to $R^2 = 0.68$) (data not shown), indicating that a minority of animals tended to eat faster when involved in successful competitive interactions. Despite their overall eating rates being moderately consistent, these animals tended to increase eating rates during times when competitive interactions increased. Figure 2.4 shows the animals

with the two strongest relationships between feeding rate and SCI. The arrows indicate where increases in rate (height of bars) corresponded to SCI increases (color intensity).

Bunk Attendance Duration. A moderate relationship was found between BA duration and SCI ($R^2 = 0.45$, $P < 0.0001$). The hourly relationship between BA duration and SCI was strongest between 0900 and 1000 (the hour of morning feeding) ($R^2 = 0.71$, $P < 0.0001$) and remained moderately strong until 1400. The weakest relationship was noted between 1500 and 1600 (the hour in which the last feeding occurred) ($R^2 = 0.24$, $P = 0.02$) (Figure 2.2). In terms of individual animals, the relationship between BA duration and SCI was highly variable, with 58% of the animals having R^2 values above 0.4 (Figure 2.3b).

Bunk Attendance Frequency. A moderate positive relationship was found between BA frequency and SCI ($R^2 = 0.49$, $P < 0.0001$). The hourly relationship for BA frequency followed a similar, but stronger overall pattern to that of the hourly relationships between DMI and SCI (Figure 2.2). The strongest hourly relationship between BA frequency and SCI was noted between 0900 and 1000 (the hour of the morning feed delivery) ($R^2 = 0.90$, $P < 0.0001$) and the weakest was between 1800 and 1900 ($R^2 = 0.47$, $P < 0.0001$). In terms of individual heifers, the relationship between BA frequency and SCI was very strong, with 96% of the animals having R^2 values ranging from 0.6 to 0.9 (Figure 2.3c).

Individual feeding strategies

A small subset of heifers (7%) ate very quickly, usually in the morning and late evening; these animals had low to moderate SCI (Figure 2.5a). Conversely, approximately 40% of the heifers varied their intake rate and SCI dramatically across the day. These animals typically had low to moderate SCI (Figure 2.5b). Approximately half of the animals maintained a relatively constant eating rate (Figure 2.5c). These animals typically had moderate to high SCI and ate fairly constantly throughout the day. Finally, the remainder of the animals engaged in a completely

different strategy by simply shifting their feed consumption to non-peak feeding times (Figure 2.5d).

Discussion

While it is commonly accepted in the literature that BW and dominance status are positively correlated, studies that make these conclusions have small sample size (i.e. Stricklin et al., 1980) and others are based on herds of dairy cattle (i.e. Phillips and Rind, 2002) and bison (i.e. Roden et al., 2005) that were of varying ages. It has been suggested that age is actually more predictive of an animal's social status in a group than its actual mass (Bernstein, 1981; Wierenga, 1990). We failed to observe a relationship between SCI individual BW in our study. This may be for a number of reasons. First, our animals were all very similar in age, thus making differences in size minimal. Second, dominance is typically assigned via physical displacements; physical contact lends itself inherently towards higher ranking. However, we considered non-contact instigations, as well as defending feeding position when instigated upon in our classification of success. These behaviors are likely to be displayed by most of the animals in the group, and not just the heaviest ones. Thus, even animals with lower BW that might be less likely to compete physically or instigate interactions may have SCI values similar to that of a heavier animal.

The high level of competition seen in this study can be attributed to the fact that only 2 out of 15 heifers (13%) could eat simultaneously (equivalent to 7 cm of bunk space per heifer). This level of overstocking at the feed bunk area is dramatically higher than that described in other studies, as well as the 20 cm recommended for typical feedlots. The highly restricted bunk space likely resulted in the increased frequency in interactions observed. For instance, in a study examining the effects of stocking densities on feeding behavior, Huzzey et al. (2006) found increased competition when 34% of the dairy cows could eat simultaneously (21 cm per head). Furthermore, Longenbach et al. (1999) compared the feeding behavior of 11.5- to 15.5-mo-old

dairy heifers in a non-competitive feeding environment to those in an environment where 55% of the animals could feed simultaneously (15 cm per head); the latter animals had significantly more, shorter eating bouts compared to those fed in the non-competitive environment; furthermore, the competition levels tended to last longer following feed delivery in the latter group. In a competitive environment, animals will experience an increased number of interruptions. This may explain why some animals in our study attempted to gain access to the feed bunk over a dozen times within a given hour.

Relationship between successful competitive interactions and feeding behavior

Although commonly utilized to assess dominance status in a group, the use of displacements at the feed bunk has been criticised because it might not be indicative of the overall competition level of the group and the individuals within it (Lobato and Beilharz, 1979; Phillips, 1993). Our SCI measure also focused on interactions at the feedbunk, but we did attempt to refine this measure by including the non-physical interactions expressed during competition as well as coding the non-instigating animals that successful defended and maintained their eating position as being competitively successful. This refinement allowed us to illustrate that animals develop strategies other than physical aggression to gain access to feed.

Familiarization with individuals through repeated encounters establishes an individual recognition of each group member, based on the different observed cues (Stookey and Gonyou, 1998; Kristensen et al., 2001). Taking into account subtle behaviors associated with the prevention of competitive interactions may also provide further insight into the social environment of a group (Kondo and Hurnik, 1990; Fraser and Broom, 1997). For instance, lower ranked animals have been noted as being the 'peacekeepers' of a group where they exhibit subtle reaction-based behaviors such as tolerance and avoidance (Fraser and Broom, 1997). Moreover, the potential exists for excluding entire segments of a population if only instigated aggressive behaviors are

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considered. Thus, studying all competitive behaviors and not just physical aggression at the feeding area likely strengthened our assessment of how social competition between individuals affected the feeding behavior of the heifers in this study.

It has also been suggested that competitive behavior observed at water stations and prime resting areas, as well as the distribution of allogrooming activities, may give much more insight into the overall competitive environment of a group of cattle, rather than feeding behavior alone (Fraser and Broom, 1997). Although we were unable to collect these data we suggest that future work is needed which examines all the other possible areas of competition in a feedlot pen.

DMI. Using the average weight of the heifers in the current trial, NRC (2000) equations predict a DMI range of 11.0 to 11.9 kg d^{-1}, which was similar to the DMI of 10.7 ± 2.1 kg d^{-1}, observed in the present study. The high standard deviation observed in our study would undoubtedly decrease if DMI were calculated over a longer period than the 3 d used in this study. Bevans et al. (2005) showed that in heifers gradually adapted to 65% concentrate, the DMI variation over a course of 3 d ranged from 1.76 to 2.65 kg d^{-1}. It has been suggested that using at least 35 d of feed intake data will give an accurate estimate of average DMI (Archer et al., 1997; Wang et al., 2006). In addition to the temporal consideration, the level of competition within the pens likely also yielded a highly variable DMI. As demonstrated by Friend (1977), a severely competitive environment may result in decreased DMI. Conversely, our heifers achieved similar DMI to that of steers of similar age and weight when provided with 93% less space per animal (Choat et al., 2002). Thus, on average, competition over the 3 d period of our study did not alter the average DMI of the heifers. Nonetheless, other studies indicate that a high level of behavioral variability exists between groups of animals (i.e. Sherwin, 1990; Benus et al., 1991), making it probable that increased competition may result in DMI decreases that are not proportional across the group.

The moderate positive relationship between DMI and the number of SCI suggests that a heifer's DMI is affected in part by the degree of competition in which she is involved. Since it is normal for DMI to vary between days (Schwartzkopf-Genswein et al., 2004; Huzzey et al., 2007), the positive relationship between these variables would likely be strengthened if more than 3 d were used in the comparison.

The weak overall daily relationship masked the very strong relationship observed between 0900 and 1000, the very weak relationship between 1400 and 1500, as well as the spike in the positive relationship associated with the last feeding. The high variability in hourly feeding behavior can be explained in part by two factors. First, although the animals in this study were fed ad libitum, few animals tended to feed in the early morning hours. That others have also found similar eating patterns (Gonyou and Stricklin, 1981) is likely due to this time period being associated with peak rumination in cattle (Wilson and Flynn, 1976). Other studies have demonstrated that cattle are highly motivated to eat following the first feed delivery of the day (Winter and Hillerton, 1995; DeVries and von Keyserlingk, 2005). Motivation is a process that describes the force and persistence an individual is willing to devote towards achieving a goal, which may include overcoming internal and external factors (Toates, 1986). In the present study we observed a strong relationship between DMI and SCI following the morning feed delivery, indicating that the heifers were likely highly motivated to compete for access to feed. This finding is supported Schütz et al. (2006) who reported that feed deprivation for 3 h resulted in cattle (especially the lighter animals in the group) exhibiting an increased motivation to feed.

Upon feeding, a number of mechanisms trigger satiation; these include oral stimulation, gastric and intestinal fill, and nutrient release into the bloodstream (Lindström, 2000). As individuals become satiated, motivation to feed decreases. Therefore, as the time increases from fresh feed delivery one would predict fewer feed-related competitive behaviors, which was indeed what we observed in the present study. Lindström and Redbo (2000) suggest that different types of

hunger may exist; an animal may physiologically be hungry, or it may possess a psychological need to perform oral manipulation of feed. According to Redbo (1992), an innate minimum duration of time spent feeding may be required for an individual to receive the necessary negative feedback to curb feeding motivation. This may in part be the reason why individual animals vary considerably in terms of when they eat, their frequency of eating and the length of time they eat at any one time in the day.

A second factor explaining the highly variable hourly feeding behavior is the diurnal feeding pattern of cattle. Cattle housed outdoors are crepuscular (Albright and Arave, 1997), typically consuming the largest amounts of feed at sunrise and sunset (Kautz-Scanavy and Stricklin, 1983; Stricklin and Kautz-Scanavy, 1984). Gonyou and Stricklin (1981) showed 2 peak feeding times at 0900 and 1900, as well as a smaller peak at 0200. Further work demonstrated that some animals were more likely than others to eat in the middle of the night (Stricklin and Gonyou, 1981). In a study examining groups of related and unrelated cows and heifers, Swanson and Stricklin (1985) suggested that such eating patterns may be due to the inability of some animals to deal with social pressures. Furthermore, as shown by Hahn (1999), animals typically reduce their DMI during high temperatures typical of mid-day. Although we did not measure ambient temperature, this experiment was conducted during the summer months when temperatures were often elevated in mid-day. The heifers in our study followed Hahn's pattern. The feed deliveries at 1230 and 1530 triggered slight increases in feeding behavior in the hour following feed delivery. This agrees with dairy cattle research showing that the delivery of fresh feed increases feeding behavior (Wierenga and Hopster, 1991; Winter and Hillerton, 1995; DeVries and von Keyserlingk, 2005). The increase in feeding behavior at midday feeding was not paired with increased competition.

The relationship between individual DMI and SCI varied greatly, but most animals relied at least in part on SCI to gain access to feed. Interestingly, animals exhibiting a weak relationship

between SCI and DMI still had similar daily DMI to those animals who exhibited a strong relationship. This indicates that social status of animals in a group is less important than a specific feeding strategy with regards to overall access to feed. The heifers in this study appeared to use individual feeding strategies; over half of the animals heavily relied on competitive interactions at the feed bunk but approximately 20% did not. This provides further evidence that assigning status to an animal based on its competitive or aggressive interactions may be too simplistic. For instance, it has been suggested that the level of aggressiveness in pigs does not necessarily predict individual coping mechanisms developed towards a competitive situation (D'Eath and Burn, 2002). Our work is the first to show the large inter-animal variation in eating strategies in cattle. Further work is needed to examine the impact of different feeding strategies on the long-term health and performance of individuals.

Eating Rate. There was no relationship between SCI and eating rate. However, the highly competitive situation did result in a higher eating rate (215 g min^{-1}) than that reported in earlier work. This rate is twice that reported for competitively fed dairy cattle fed rations containing similar amounts of forage. For instance, Olofsson (1999) showed an average rate of 93 g min^{-1} when 8 cows were given access to 2 feeding stations (23 cm per cow, over three times the amount of space allotted to our heifers). The rate in our study was also higher than that previously reported for competitively fed steers (average of 124 g min^{-1} for 15 steers to one feeding station; Gonyou and Stricklin, 1981). However, it should be noted that the latter study provided animals with protection in the form of stanchions that would prevent the physical removal of one animal by another from the feeder. The fact that the feeding system used in our study did not have stanchions or any barriers associated with the feeder may have resulted in the increased eating rates observed. Previous work on dairy cattle has shown that barriers at the feedbunk lower aggression and displacements (Endres et al., 2005; DeVries and von Keyserlingk, 2006; Huzzey et al., 2006).

Individual animals varied considerably in their average eating rate (min. 91 g min^{-1}, max. 499 g min^{-1}), with some individuals averaging eating rates of 561 g min^{-1} over certain periods. Although these rates are high, others have reported eating rates double these (Clough, 1972). As competition increases, the consequent decrease in feeding time increases the rate of intake (Hafez and Lindsay, 1965; Gonyou and Stricklin, 1981;). Even when this is borne in mind, some animals displayed substantially higher average eating rates than others, suggesting that animals may develop different coping strategies when faced with a highly competitive feeding environment. Animals classified as 'subordinate' were more likely to alter their consumption rhythm (Hopster and Wierenga, 1986), thereby increasing their eating rate compared to 'dominant' animals (Harb et al., 1985). Since overall intakes often remain similar between animals even when feed access is restricted (Shaw, 1978; Harb et al., 1985), other factors must be influencing feeding behavior. Therefore, we hypothesized that competitively successful animals had lower eating rates compared to their less successful counterparts, on the basis that the latter would be able to increase their eating rate in response to the increased risk of being displaced from the feeding area. A small cohort (6%) exhibited moderate to strong relationships between their individual eating rate and SCI, indicating that some animals were indeed able to eat faster when engaged in competition. However, the remaining animals showed weak to no relationship between individual eating rate and SCI. Our results are the first to show that the overall successfulness of animals at the feed bunk does not have a great impact on overall eating rate, but a few individuals do appear to be able to alter their rate of intake based on competition.

Since previous reports have indicated that animals are highly motivated to eat following the delivery of fresh feed (DeVries et al., 2005), we predicted a stronger relationship between eating rate and SCI at certain times of the day, such as immediately following delivery of fresh feed. Surprisingly, no overall group-based relationship was found. The minority of the animals that did exhibit a relationship between eating rate and SCI may have been motivated to do so by hunger.

Early morning feed deprivation associated with a high motivation to feed encouraged competitive behavior in animals that may otherwise avoid competitive interactions in order to gain access to the feeder. Rutter et al. (1987) found that, when hungry, animals typically classified lower in rank may act more competitively in order to access feed. Some of the animals in our study appeared to compensate in part by increasing their eating rate (Figure 2.4). Kenwright and Forbes (1993) found that animals classified as lowest in terms of herd dominance increased their rate of eating during the 40-min peak periods after each milking, and spent less time eating overall, while the most 'dominant' cows did not alter their feeding behavior. It appears that some less competitive animals will only use competition to access feed at times when feeding motivation is highest. Olofsson (1999) showed that cows classified as 'subordinate' altered their intake pattern and fed more frequently during the less preferred hours of the day. Over 20% of the animals in our study had a negative relationship between eating rate and BA duration; in other words, they showed a tendency towards increasing their eating rate as their available feeding time decreased (R^2 ranging from $0.12 - 0.27$, $P = 0.05$; data not shown). It would be advantageous in future work to look at such animals over a larger number of days to see if this negative relationship between duration and rate becomes stronger.

Around times of increased motivation, the animals with increased eating rate had weak relationships between BA duration and SCI. This suggests that even when these animals were competitively successful, they still had shorter feeding durations, likely because they were displaced quickly. It appears some individuals avoid engaging in social interactions at the feed bunk unless highly motivated to feed, at which point they eat quickly, and have shorter and more frequent visits. This is supported by Ketalaar-de Lauwere et al. (1996) who reported that 'dominant' cows made fewer visits to the feeding area. Overall, the failure to observe a strong relationship between individuals' eating rate and their SCI indicates that, although important at

certain times, and specifically to certain heifers, eating rates of the majority of the group did not alter based on the level of competition.

Bunk Attendance Duration. The overall BA duration in this study (62 ± 22 min d^{-1}) was low compared to the feeding duration of grazing cattle (i.e. 240 to 540 min d^{-1}; Taylor and Field, 1998); however, the animals in this study were eating a diet much higher in energy than grazing animals, allowing for less time spent eating to attain a similar amount of energy. In other studies where cattle were eating high-energy diets, dairy cattle spent 198 to 243 min d^{-1} eating (Olofsson, 1999) and beef cattle spent 141 min d^{-1} eating (Schwartzkopf-Genswein et al., 2004). This may be explained by the fact that the feeding system used in the present study only allowed two heifers to feed at once and dramatically increased competition. Typically animals are provided with at least twice the bunk space per animal (Zinn, 1989; Gunter et al. 1996) as in our study, where the increased competition likely necessitated that all animals spend less time eating. In a trial where 15 animals were restricted to one feeding station, average bunk attendance durations ranged from 78 to 87 min d^{-1} (Gonyou and Stricklin, 1981). Of further interest was the high level of BA duration variability between animals (min. 22 min d^{-1}, max. 108 min d^{-1}), possibly indicating that some animals were better able to cope with the restricted bunk space than others, either by shifting their eating times, or simply becoming more competitive.

The moderate relationship between BA duration and the number of SCI suggests that animals that are more successful in their attempts to gain access to feed may be able to eat longer before being displaced. Olofsson (1999) reported a similar finding when observing dairy cattle fed in a competitive environment. DeVries et al. (2004) reported that animals which were displaced most often showed the greatest increase in feeding time when provided with 100 cm of feed bunk space, versus 50 cm. Our results suggest that BA duration was strongly influenced by the competitive successfulness of an individual at certain times of the day compared to others. Not surprisingly, the strongest relationships were noted in the morning when cattle are highly

motivated to move towards the feed bunk immediately after delivery of fresh feed (DeVries et al., 2005). Although early morning is also associated with increased feeding behavior (Ray and Roubicek, 1973; Gonyou and Stricklin, 1981), few animals visited the feed tubs prior to the 0900 feed delivery, perhaps because they were accustomed to feeding in the morning only upon feed truck arrival.

In terms of individuals, almost 30% of the animals exhibited a strong relationship between time spent at the bunk and their SCI. In our study animals were fed a backgrounding diet high in forage and low in grain, making over-consumption of feed, during a large meal or one that is eaten quickly, less likely. Further, although we did not measure sorting behavior, the highly competitive environment likely discouraged any sorting behavior (in favour of the grain), indicating that rumen health was likely not affected. However, lack of time spent at the feedbunk may be a significant factor in feedlot settings where animals are receiving high-concentrate finishing diets. Large meals, eaten quickly, have been linked to variable eating patterns and large pH declines (Fanning et al., 1999). Variable feeding behavior has been linked to increased morbidity (Sowell et al., 1999). Therefore, it is important to determine the complexity of the feeding strategies animals use in order to gain access to feed, not only in terms of competitive behaviors, but also in terms of feeding duration, rate and the number of visits to the feed bunks.

Bunk Attendance Frequency. Previous work on the feeding behavior of beef cattle has relied on the use of a meal criterion to objectively calculate the total number of meals (e.g. 300 s inter-meal interval; Schwartzkopf-Genswein et al., 2002) but this approach would not allow us to assess the impact of competition on the outcome of a single visit. Tolkamp et al. (2000) concluded that meals were a more biologically relevant unit of measure for feeding behavior; the authors indicated that visits were not relevant because they were dependent on a variety of variables, including hierarchy of the group, social pressures and feeder construction. However, the aim of our study was to take into account all individual competitive feeding behaviors and their subsequent

outcomes. We also felt that meals were more relevant when using daily data, as hourly data were too variable. Consequently, we chose to use individual BA frequency rather than meals. BA frequency assessed whether the animal was successful in maintaining its feeding position or whether another animal displaced it. Every successful feed bunk access was associated with 1.54 SCI over the course of the day. We observed a relatively high number of interactions compared to other studies (i.e. Olofsson, 1999; Huzzey et al., 2006); this was likely due to the severely restricted feeding space per animal, as well the definition we used to classify interactions. DeVries et al. (2004) indicated that as feeding space increased, feeding activity increased and competition (defined as displacements) decreased, particularly when feeding motivation was high. Therefore, it is likely that if more bunk space were available, the ratio of SCI to visits would drop considerably.

The strongest feeding behavior/social relationship was observed between BA frequency and SCI, with the majority of bunk visits associated with at least one SCI. This indicates that the more times an animal attended the feed bunk, the more likely it was to have an SCI. Some appearances at the feed bunk occurred without any SCI. Although Hicks et al. (1989) reported that 7.5 to 20% of cattle might not feed in any given 24-h period, this did not happen with any of the heifers used in our study.

Individual feeding strategies

Larson et al. (1992) cautioned the scientific community against the use of group-averaged data to avoid the risk of masking important individual animal variation. This observation has relevance in our study as animals used distinctly different coping strategies to gain access to feed in a competitive feeding environment. The data from an hourly and individual animal perspective illustrated sources of variation in competitive behavior. For instance, the relationship between feeding behavior and competition was very strong during the first hour following feed delivery, but owing to the masking effect of averaging data, the overall relationship between these two variables

was weak. Furthermore, even though no overall relationship existed between eating rate and competition, individual analysis showed that a small minority of animals increased their eating rate when faced with competition. These examples demonstrate that hourly and individual variation is lost when the data are averaged. It should also be noted that since competition was extremely high, differences in individual feeding rates may have been masked. Further studies are needed to study the variability of eating rates in cattle fed in a commercial setting with the recommended 20 cm of feed bunk space for finishing cattle (Feeder Association of Alberta, 2002).

Of further interest in terms of individuality is the phenomenon of tandem eating. Similar to the "cooperative eating" behavior noted by Stricklin and Gonyou (1981), our study also found situations in which animals ate cooperatively. For instance, two heifers were typically seen at a feed tub together, and routinely shared access to it. Although each heifer would wait for the other to back out before gaining access to the respective feed tub, one was often observed eating quickly while the other ate slowly. Furthermore, when these two heifers ate together, they were involved in fewer SCI than when they ate separately. Craig (1986) noted that alliances between individuals could impact the social environment. Therefore, behavioral differences do not only exist between individuals, but certain individuals also develop cooperative strategies in their feeding behavior.

Arnold and Grassia (1983) were among the first to discuss the potential importance of individual behavior in beef cattle. The heifers in this study showed individuality in their behavioral approach to feeding. As has been demonstrated in some primatology studies focusing on individual behavior over three decades ago (Deag, 1974; Hinde 1978), the intricacies of group social order are governed by much more than simple social rankings (Reinhardt, 1983). The concept of individuality in cattle is rarely considered and is frequently lost in studies focusing on hierarchical ranks within a group. Manteca and Deag (1993) suggest that individuals perform a 'social role' within a group; awareness of such roles is not implicit (Hinde, 1974), but rather animals simply take on roles predetermined by genetic and external factors. Feeding behavior of individuals will

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vary depending on their overall social role, as well as the individual power and leverage they hold within the group (Lewis, 2002). Considerable variation exists in the individual feeding behavior of cattle in a competitive environment. Although we have shown that some of this is linked to competitive behavior, it is clear that much of the variability between individuals is not. Animals develop individual feeding behavior that may or may not include competition. Therefore, research which focuses on the social environment's impact on feeding behavior should take into account individual behavioral differences. Social status of animals should be assessed by more than just instigated displacements, as this method only assesses the successfulness of the physically aggressive animals, and does not consider non-physical and defensive interactions.

Implications

Feedlot animals are typically provided with less feed bunk space than would be required for all the animals to feed simultaneously. Such spatial constraints create increased demand on resources such as feedbunk space. It has been suggested that the resulting competition for feed may impact certain animals more negatively than others. We found that the amount of successful competitive interactions in which an animal was involved did influence its ability to gain access to feed, and to a lesser extent, the amount of feed it consumed. The importance of competition varied throughout the day, indicating that motivation level impacted an animal's competitiveness. In addition, reliance on successful competitive interactions varied greatly between individual animals. Distinct differences in both social and feeding behavior were found. Certain animals were less inclined to compete and instead altered their feeding behavior in order to gain access to feed. In a feedlot environment where feed is not typically available ad libitum, those animals with altered feeding behavior may be at a disadvantage in terms of access to the amount of feed they need. Future work is needed to assess how those animals less likely to instigate competitive interactions function in a typical feedlot environment; it is currently unclear whether such animals suffer in terms of health and performance.

Table 2.1. Competitive behaviors and potential outcomes of beef feedlot heifers (n=45) provided access to two individual feeding tubs

Competitive Behavior	Outcome	Coding
Instigator either: • Makes contact with its head to the reactor's shoulder/stomach/rump (not directly from behind as this could be scratching)	1. Reactor moves and instigator gains access to feed tubs	Instigator coded successful
• Approaches reactor, but makes no physical contact with reactor	2. Instigator is unsuccessful at gaining access to feed tubs	Reactor coded successful

Table 2.2. Descriptive statistics of feeding behavior (DMI, eating rate, bunk attendance duration and frequency and successful competitive interactions for 3 pens of 15 animals provided feed three times per day through two individual feeding stations)

	Mean	SD	Min	Max
Initial weight, kg	520.5	32.2	440	586
Daily[a]				
DMI, kg d^{-1}	10.7	1.6	7.6	15.4
Rate, g min^{-1} d^{-1}	214.8	89.1	91.6	498.9
BA Duration, min d^{-1}	61.9	21.6	21.5	108.3
BA Frequency[b], per d	55.6	13.9	28.7	92.0
SCI[c], per d	86.0	31.2	35.3	167.7
Hourly[d]				
DMI, kg h^{-1}	0.74	0.13	0.51	1.0
Rate, g min^{-1} h^{-1}	226.5	98.9	91.3	561.2
BA Duration, min h^{-1}	4.1	1.5	1.3	8.1
BA Frequency[b], per h	3.9	1.0	2.1	6.2
SCI[c], per h	6.4	2.3	2.7	12.3

[a]Data were averaged daily for each animal.

[b]BA Frequency. A new bunk visit was counted any time an animal left feed tub and returned

[c]SCI = successful competitive interaction (includes displacement by instigator and defence by reactor)

[d]Data were averaged for every hour (13 h) separately for each animal

4.3 m

1.3 m

3.6 m

3.1 m

Not Directly Feed Related

Directly Feed Related

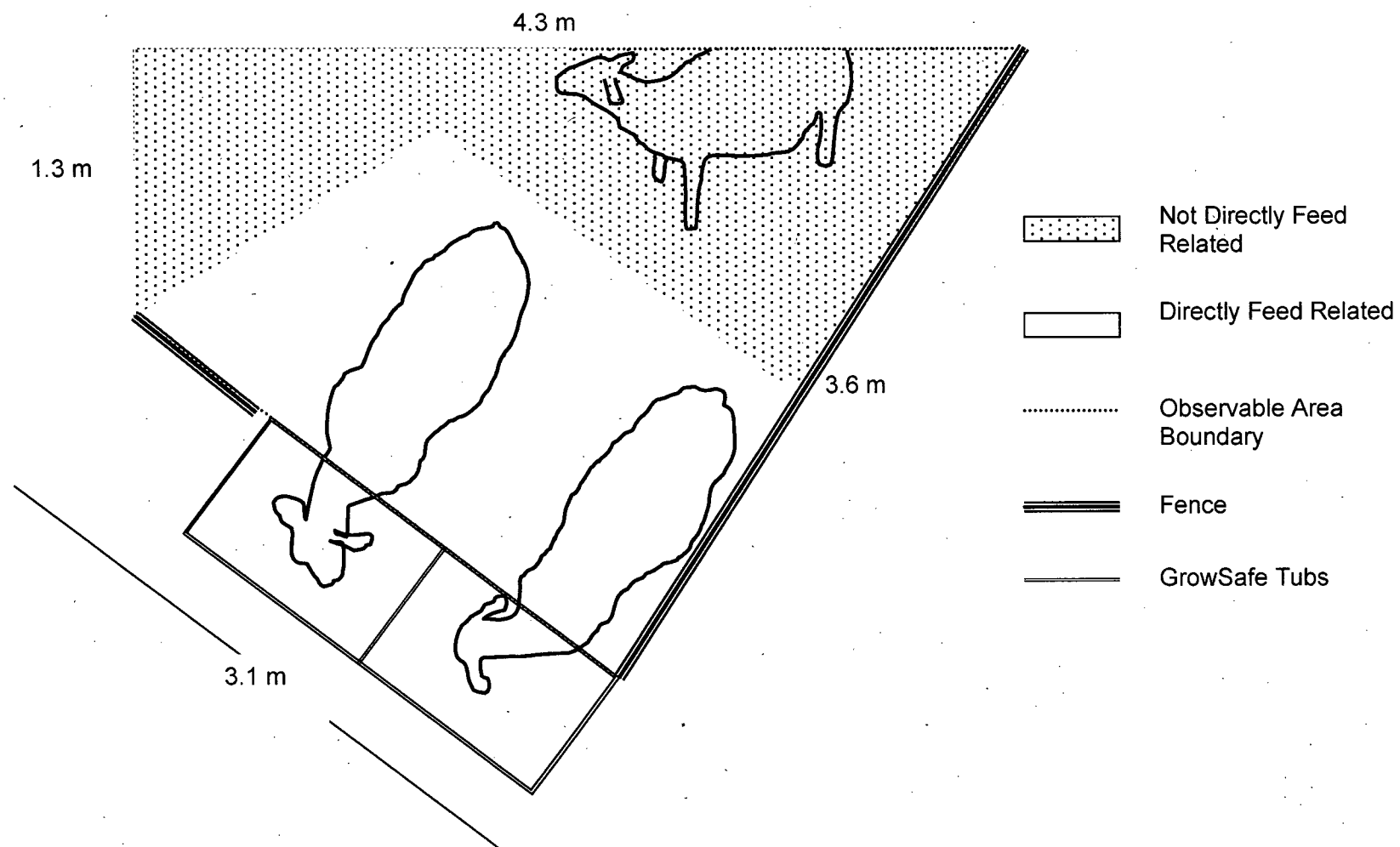Observable Area Boundary

Fence

GrowSafe Tubs

Figure 2.1. Area of observation used for coding competitive behaviors. Only "directly feed related" area was coded.
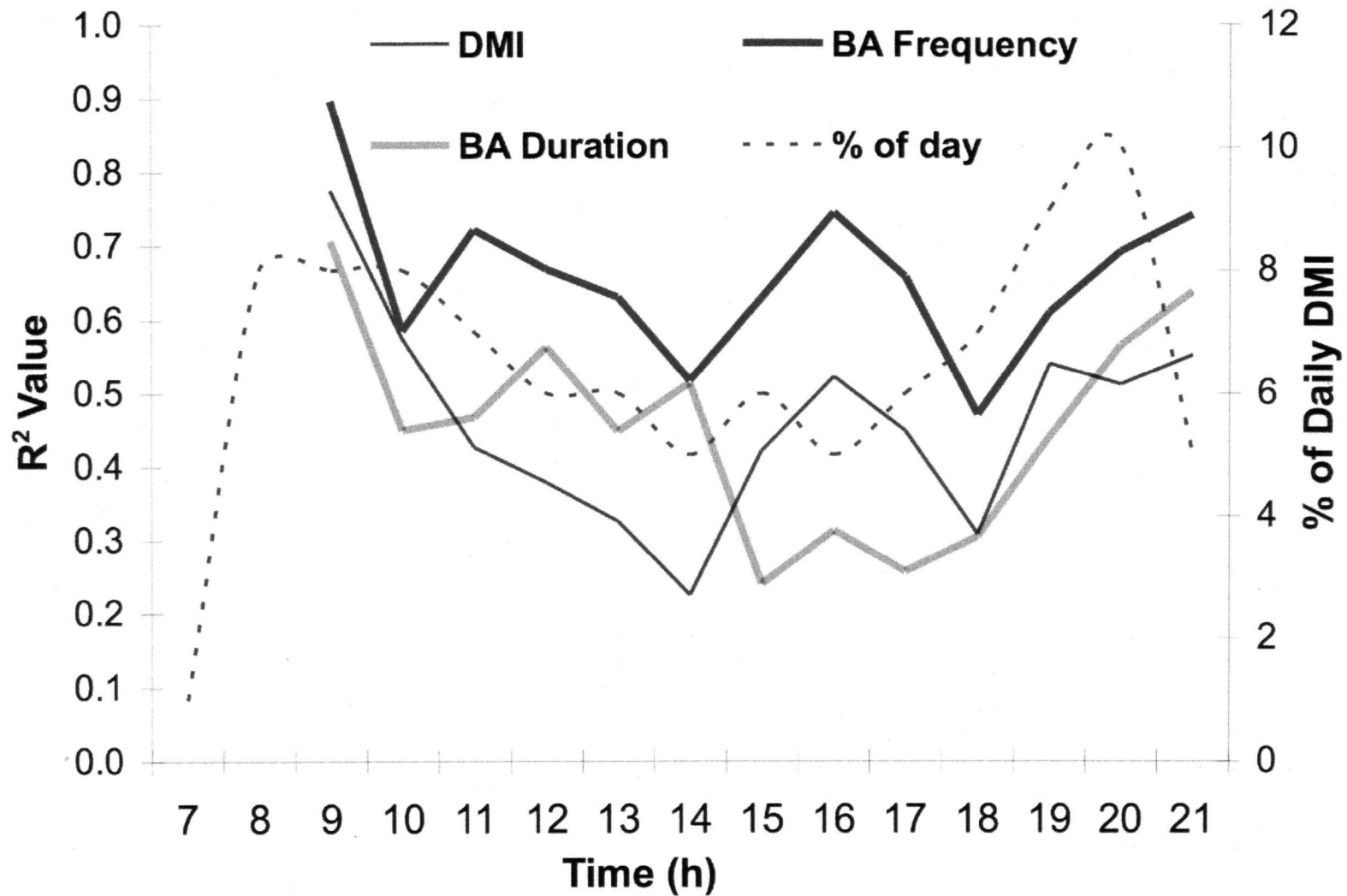
Figure 2.2. Generalized linear models for hours 0900 to 2100, for dry matter intake and successful competitive interactions (black), bunk attendance frequency and successful competitive interactions (gray), and bunk attendance duration and successful competitive interactions (light gray). Percent of daily DMI consumed in each hour is shown on the secondary Y-axis (dotted line). Data were averaged for 3 days for 45 heifers (three groups of 15) fed three times a day.

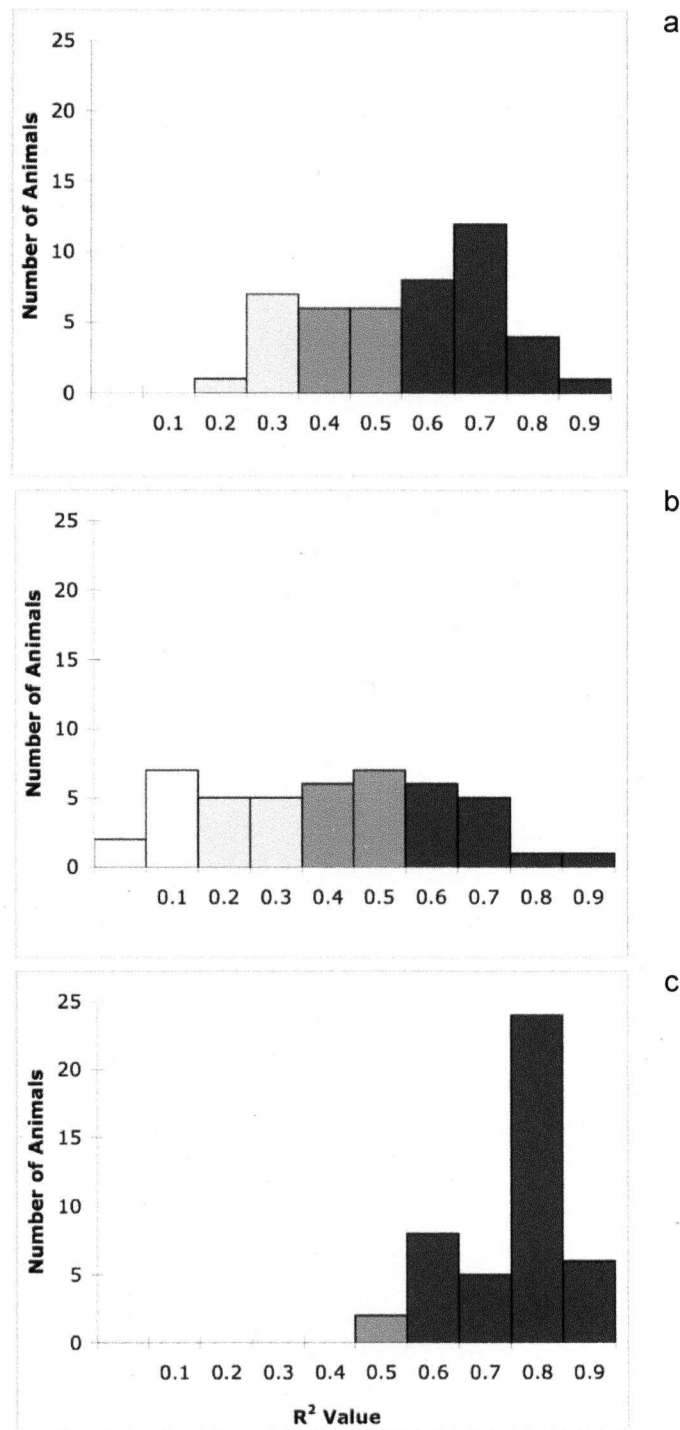Figure 2.3. R^2 values from generalized linear models using individual animals for, a) dry matter intake and SCI; b) bunk attendance duration and SCI, and c) bunk attendance frequency and SCI. Too few relationships existed for eating rate and SCI. Colors indicate strength of relationship: Strong ($R^2 > 0.6$) dark gray; Moderate ($R^2 = 0.4$ to 0.59) medium gray; Weak ($R^2 = 0.2$ to 0.39) light grey; and None ($R^2 < 0.2$)
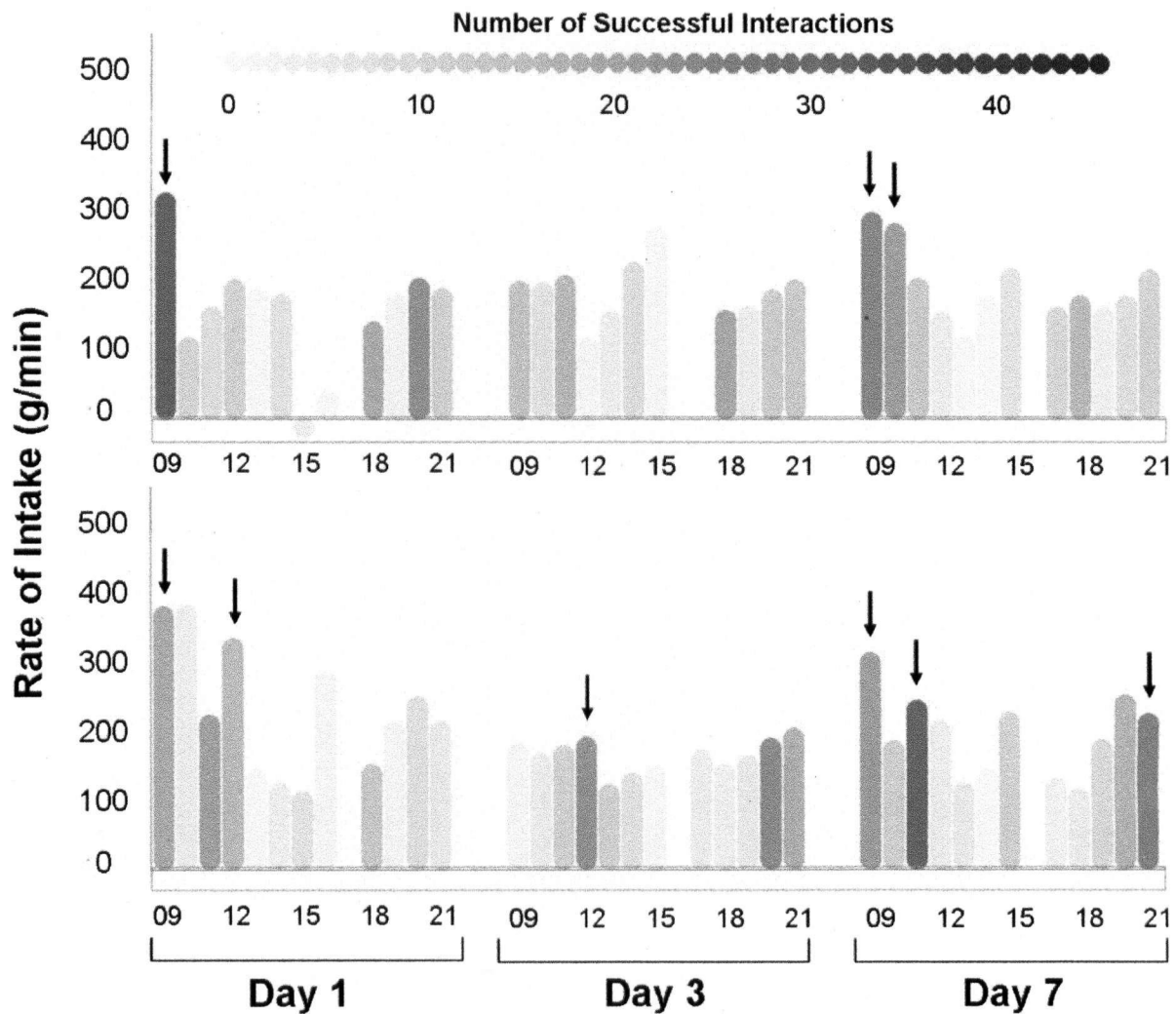
Figure 2.4. Two animals with the strongest relationship between their feeding rate and their SCI (R^2 = 0.68 and 0.65, P = 0.0001). Animals were fed at 0900, 1200 and 1500. Eating rate is indicated by height of bars, and number of SCI is indicated by color intensity of bars. Arrows illustrate examples of increased rates corresponding to larger numbers of SCI. Dots below x-axis indicate a SCI that did not result in any actual intake.
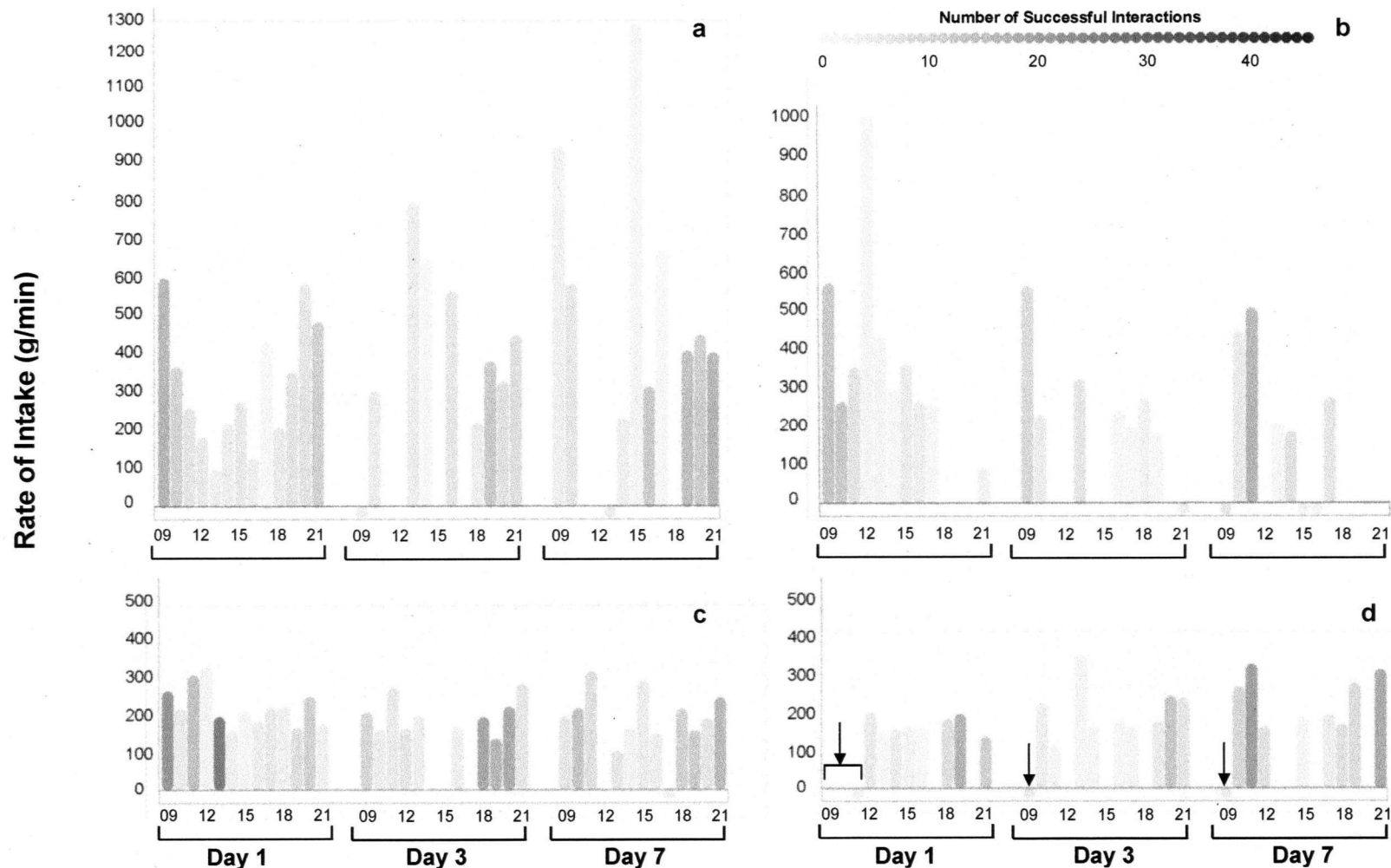
Figure 2.5. Individual feeding strategies: a) heifers ate very quickly, especially in morning and late evening, with low to moderate SCI (7% of group); b) heifers varied intake rate and SCI dramatically across the day (39% of group); c) heifers developed and maintained relatively constant eating rate, with moderate to high SCI (47% of group); d) heifers tended to eat at different times (indicated by the arrows), with primarily low SCI (7% of group). Animals were fed at 0900, 1200 and 1500. Dots below x-axis indicate an SCI that did not result in any actual intake.

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CHAPTER 3: GENERAL CONCLUSION

The first published work investigating social behavior in cattle focused on the effect of horns on social "rank" within the herd (Woodbury, 1941). Over a decade later, Schein and Fohrman (1955) introduced the concept of 'social dominance' in a herd of cattle and are still frequently cited in today's literature. Despite their major contribution to the literature, the following statement by Schein and Fohrman (1955, pg 45) - "Few investigators have recognized the distinction between a group pattern and a group of individual behavior patterns" - often goes unmentioned despite its potential applicability to the social behavior of cattle housed in groups.

The historical emphasis of describing group patterns rather than individual patterns may have arisen, in part, from the practicality of studying the group as a whole rather than the individuals within the group. Monitoring individual behavior within a large herd of cattle has traditionally been extremely time consuming and tedious; for example, even Schein and Fohrman (1955), who studied a relatively non-competitive herd of cattle at pasture, occasionally had to exclude observations of behavior because of its complexity. However, technological advances have now greatly facilitated the collection of individual behavioral patterns, particularly those related to feeding.

The goal of this thesis was to describe how competition affects the individual feeding behavior patterns of beef cattle housed in small groups. Unlike previous work to date, we were able to capture detailed hourly feeding behavior of individual animals. The technology available enabled me to retrieve hourly behavior and feed intake data to within 0.3 kg accuracy for individual animals within a highly competitive environment. In addition, the availability of high-resolution color digital cameras made monitoring detailed interactions between animals easier and more accurate. Combining these detailed interactions with the feeding behavior data provided detailed insight into how individual animals cope in a competitive environment over the entire day,

when factors such a feed delivery and motivation to feed change continually. This work showed that, when faced with a competitive feeding situation, individuals developed various strategies other than direct physical aggression in order to gain access to feed. Clearly, categorizing animals as dominant, or by assigning ranks based only on physical displacements at the feedbunk, does not fully incorporate the individual behavioral differences between individuals within a group.

The results arising from my research confirm the importance of the individual's contribution to the development of the overall social group environment. We can only speculate at this time on the reasons for differences between individuals, but it appears that animals differed in their feeding motivation, and as a result employed different strategies to access feed, which also resulted in different strategies being employed throughout the course of the day. For example, some of the animals in my study were equally successful in accessing feed, but rather than competing with con-specifics they elected to shift their eating to less desirable times in the day. Of further interest is the tendency for many animals to eat dramatically faster, but only during times of high motivation to feed. It became clear that competition was only one piece of a complicated social structure that develops as competition increases.

All animals play a certain role within a group, and it is important to show the individuality of those that make it up. The variation between animals is a point that has rarely been considered in previous literature that categorizes animals in terms of 'dominance' status. Rather than focusing on animals as a group, future work should really begin to investigate the impact of the variation of behaviors between animals on the *welfare of the individual.*

Despite its benefits, the detail of my data did complicate its interpretation. The majority of previous studies have collected daily feeding behavior, and have classified animals categorically; unfortunately, this method arguably removes a great deal of the variability in individual behavior. Moreover, my decision not to categorize animals into social ranks made comparison with previous literature difficult, in that I lacked similar definitive concluding statements. For instance, previous

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work has suggested that animals classified as 'subordinate' eat at less preferred times of the day (Stricklin and Gonyou, 1981), but my interpretation of the results obtained from the study described herein questions such a 'linear' approach. In order to classify an animal into any category, it has to be assumed that the established social hierarchy is representative of an individual's *overall role* in the group. Unfortunately, these social hierarchies do not consider that competitiveness and aggressive behaviors vary based on the motivational situation of an individual. Therefore, assigning classification of dominance to individuals masks the potential individual strategies animals may develop.

Therefore, even though I was not able to state that 'dominant' animals had specific characteristics over 'subordinate' ones, the results obtained in the study described in Chapter 2 provide a number of lines of evidence for how variations in individuals' competitiveness impact the individual as well as others in the group throughout the day. Successful competitive interactions positively influence the amount of feed an animal is able to access, and how long that animal is able to feed, as well as how many times the animal must visit the bunk. Interestingly, the relationship between competition and these feeding behavior variables varies immensely in the course of a day, indicating that motivation to feed plays a major role in dictating the level of competition that is used by an individual. Moreover, the individual differences in strategies employed by individuals within the group to gain access to the feed described in this thesis provide the first evidence that the social behavior of beef feed lot cattle is extremely complex, and more research is required to ascertain the various factors influencing how individuals react to a competitive environment.

Current feedlot management practices have continued to constrain the amount of space given to individual animals in order to maintain economic competitiveness and maximum profitability. My work demonstrates that animals presented with spatial constraints at the feedbunk alter their feeding behavior, especially the less competitive individuals. We did not observe any

injuries as a result of the competition, but this study examined only 3 d of behavior. Clearly, the risk of injuries would likely become more prevalent if animals were forced to access feed over a longer period of time in a heavily competitive environment.

Future research

Future work should include a controlled study where animals are subjected to both a competitive and a non-competitive environment. Subjecting all animals to both treatments will provide insight into how individuals cope with competition, and may also suggest the mechanism behind how and why individual behavioral differences occur. My work has indicated that variation exists between how individuals view resources, and subsequently how individuals are prepared to maintain access, as such future work should focus on more than just feeding behavior. The impact of competition on access to other resources within the pen, such a lying space and water, should also be examined in order to ascertain if the welfare of specific animals is compromised when different resources are constrained. More broadly, future research needs to focus on the importance of individuals within a group. More effort needs to be devoted to studying individual behavioral differences of animals, rather than categorizing them on the basis of the variable of 'displacements at the feedbunk'. Such work would not only provide more insight into group dynamics, but might also demonstrate how to insure all individuals within a group have equal access to resources.

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