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ABSTRACT OF DISSERTATION

John Denver Bailey

The Graduate School
University of Kentucky
2003

AN APPROACH TO THE MEASUREMENT OF
SEXUAL BEHAVIOR IN THE BULL (*BOS TAURUS*) USING VARIABLE
FEMALE STIMULUS CONDITIONS

ABSTRACT OF DISSERTATION

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy
in the College of Agriculture at the University of Kentucky

By
John Denver Bailey

Lexington, Kentucky

Director: Keith K. Schillo, Ph.D., Associate Professor of Animal Sciences

Lexington, Kentucky

2003

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AN APPROACH TO THE MEASUREMENT OF SEXUAL BEHAVIOR IN THE BULL (*BOS TAURUS*) USING VARIABLE FEMALE STIMULUS CONDITIONS

Most researchers studying sexual behavior of the bull have adopted the practice of severely restraining and sedating female stimuli, utilizing so-called “service stanchions” and quantifying behavioral events expressed by each bull. Based on these observations, bulls are classified as having high, medium, or low libido and ranked according to their ability to “service” the inanimate stimuli. It has been assumed that these methods represent appropriate measurements of reproductive behavior that will be expressed in a natural mating scenario and that bull sexual behavior can be studied in a manner that is independent of the context of the female. Hence, conventional methods fail to consider the appropriate contexts under which cattle interact sexually. Based on these issues, I investigated the role of unrestrained female stimuli in modulating the expression of male sexual behavior in domesticated bovine. Experiments were conducted to develop a paradigm for studying sexual behavior in bulls within a social setting that permits extensive interactions between males and females. The first

experiment tested the hypothesis that female novelty and receptivity interact to govern the expression of mounting behavior in the bull. In this experiment, bulls that were exposed sequentially to 4, novel, estrual females expressed more mounts with intromission than when exposed alternately to two, estrual females or to the same estrual female over a four-hour period. Bulls exposed to a non-estrual female were not allowed to mount and intromit although they readily attempted to mount. A second experiment tested the hypothesis that mounting behavior of bulls exposed sequentially to 4, estrual females in 2 hours would be the same as that in bulls exposed to a group of 4, estrual females for 2 hours. Results suggested that in group mating situations there are differences in how males distribute copulations when presented with unrestrained stimulus females sequentially. Repeatability of sexual behavior was calculated by repeatedly testing bulls paired with either single or multiple unrestrained, estrual females on 8 different occasions and calculating the intraclass correlations. Overall, repeatability was low and indicated a large environmental component. This electronic dissertation contains multimedia video files which allow the reader to visualize representative examples of sexual behavior in *Bos taurus*.

KEY WORDS: bull sexual behavior, Coolidge effect, mounting, intromission, serving capacity

John Denver Bailey

July 30, 2003

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Date

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DISSERTATION

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The Graduate School
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TABLE OF CONTENTS

Acknowledgements	iii
List of Figures	viii
List of Files	ix
Chapter One - Review of Literature	1
Introduction	1
Utilitarian Views of Bull Sexual Behavior	3
On the Ambiguity of Conventional Terminology	9
Ontogeny of Sexual Behavior in the Male Bovine	12
The Dualism of Bull Libido and Sexual Performance	15
Basic Descriptions of Bovine Sexual Behavior	17
Ethological Descriptions of Appetitive and Consummatory Sexual Behaviors	21
Subdivisions of Reciprocal Mating – Anticipatory and Preparatory Behaviors	22
<i>Anticipatory Responses</i>	22
<i>Preparatory Responses</i>	27
The Bases of Stimulus Attractivity	29
<i>Stimulus Attractivity Through Visual, Olfactory, and Auditory Perception</i>	32
<i>Summary of Stimulus Attractivity</i>	36
The Bases of Stimulus Proceptivity and Receptivity	37
<i>Affiliative Behaviors</i>	39
<i>Solicitational Behaviors</i>	40
<i>Approach and Withdrawal</i>	41
<i>Physical Contact Responses</i>	42
<i>Mounting by the Female</i>	49
<i>Female Receptivity</i>	50
The Consummatory Phase in the Bovine	52
Postcopulatory Refractoriness and Cessation of Mating in the Bovine	61
<i>The Coolidge Effect – Mythical Beginnings of a Sexual Testing Paradigm</i>	61
Other Factors Governing Sexual Behavior in the Bull	66
<i>Neuroendocrine Regulation of Sexual Behavior – The Adaptive Behavior Model</i>	66
<i>Consideration of Male to Female Ratios</i>	71
<i>Copulation Frequency Scores in Restrained Female Tests and Fertility in the Male Bovine</i>	72
<i>Social Effects and Dominance Hierarchies Among Bulls</i>	75
<i>Summary of These Additional Factors Affecting Herd Fertility</i>	75
Development of Quantitative Tests for Consummatory Behaviors in the Male Bovine	77
Development of the "Serving Capacity" Test	79
Critique of Conventional Approaches of Quantifying Bull Sexual Behavior	82
Critique of Conventional Approaches Using Ethological Perspectives	83

Critique of Conventional Methodology Using Literary Examples of Bias.....	88
Present Hypotheses Concerning Bull Sexual Behavior Utilizing Conventional Methods.....	91
Toward Novel Hypotheses Concerning Sexual Behavior of Bulls	92
Critique of Conventional Methods from an Animal Welfare Perspective	94
Summary of Critique	95
Final Summary and Conclusions.....	96

Chapter Two - The Effects of Female Novelty and Receptivity on the Expression of Sexual Behavior in Adult Male Bovine	100
Introduction	100
Materials and Methods	101
<i>General</i>	101
Males	101
<i>Females</i>	103
<i>Estrus Induction for Sexual Behavior Tests</i>	104
<i>Behavior Test Procedure</i>	104
<i>Statistical Analyses</i>	107
Results.....	109
<i>Total Mounts</i>	109
<i>Mounts with Intromission</i>	110
<i>Aborted Mounts</i>	112
<i>Mounting Interval</i>	114
<i>Flehmen Responses</i>	116
Discussion	117

Chapter Three - Effects of Serial or Group Exposure to Variable Female Stimuli on the Temporal Expression and Repeatability of Sexual Behavior in the Adult Male Bovine.....	135
Introduction	135
Materials and Methods	139
<i>General</i>	139
Males.....	139
<i>Females</i>	140
<i>Estrus Induction for Sexual Behavior Tests</i>	141
<i>Behavior Test Procedure</i>	141
<i>Statistical Analyses</i>	143
Results.....	145
<i>Total Mounts</i>	145
<i>Mounts with Intromission</i>	147
<i>Aborted Mounts</i>	149
<i>Mounting Interval</i>	150
<i>Flehmen Responses</i>	151

<i>Order of Stimulus Females Receiving Mounts with Intromission</i>	151
<i>Temporal Distribution of Mounts with Intromission among Stimulus Females</i>	152
<i>Mounts with Intromission per Female Exposed</i>	153
<i>Repeatability of Bull Sexual Behaviors</i>	154
Discussion	154
Chapter Four - General Discussion and Conclusions	175
References	180
Vita	192

LIST OF FIGURES

Figure 1. The hierarchical, linearized view of bovine sexual behavior taken from Senger (1999).....	19
Figure 2. Reciprocity in heterosexual mating in the bovine, adapted from models proposed by Pfaus (1996) (<i>Incentive Sequence Model</i>) and Beach (1976)	23
Figure 3. Distinction between anticipatory and preparatory behaviors (from Pfaus, 1996)	25
Figure 4. Diagram of the reproductive anatomy of the adult male bovine, detailing the penis retractor muscle and the sigmoid flexure	53
Figure 5. The <i>Adaptive Behavior Model</i> proposed by Bindra (1974)	68
Figure 6. Diagram (not to scale) detailing experimental procedure and apparatus for Experiment 1	124
Figure 7. Treatment by time interaction for total mounts - Experiment 1	125
Figure 8. Treatment by time interaction for mounts with intromission - Experiment 1	127
Figure 9. Treatment by time interaction for aborted mounts - Experiment 1	129
Figure 10. Treatment by time interaction for mounting intervals - Experiment 1.....	131
Figure 11. Treatment by time interaction for flehmen responses - Experiment 1.....	133
Figure 12. Diagram detailing experimental design for Experiment 2.....	160
Figure 13. Treatment by time interaction for total mounts - Experiment 2	161
Figure 14. Treatment by time interaction for mounts with intromission - Experiment 2	163
Figure 15. Treatment by time interaction for aborted mounts - Experiment 2	165
Figure 16. Treatment by time interaction for mounting intervals - Experiment 2.....	167
Figure 17. Treatment by female order interaction - Experiment 2.....	169
Figure 18. Treatment by time interaction for number of females receiving mounts with intromission	171
Figure 19. Treatment by time interaction for number of mounts with intromission per female exposed	173

LIST OF FILES

JDBDiss.pdf.....	835 KB
movie1.avi.....	8.6 MB
movie2.avi.....	10.8 MB
movie3.avi.....	3.9 MB
movie4.avi.....	6.3 MB
movie5avi.....	6.1 MB
movie6.avi.....	3.8 MB
movie7.avi.....	8.7 MB
movie8.avi.....	8.6 MB
movie9.avi.....	4 MB
movie10.avi.....	3.8 MB
movie11.avi.....	10.9 MB
movie12.avi.....	11.8 MB

Chapter One

Review of Literature

Introduction

Today, it is accepted dogma that cattle evolved under a polygynous mating system where a few, so-called dominant males mate with multiple females during periods of sexual receptivity. Mating in this species has a tendency to occur in the late spring and early summer and, based partly on adaptation to temperate environments, a spring calving scenario predominates (Spitzer et al., 1988). However, cattle are not considered seasonal breeders *per se*, as females continue to cycle year round if they are not pregnant. Nonetheless, these temperate adaptations maximize the probability that young will survive as available feed supplies during the spring increase in quality and quantity (Spitzer et al., 1988). A major goal of modern beef production is to maximize the reproductive potential of the breeding herd by utilizing management techniques aimed at ensuring that the majority of postpuberal and cycling female cattle are pregnant at the end of the breeding season. Females that are not pregnant by the end of the breeding season represent major sources of economic loss to producers of livestock (Wiltbank et al., 1961; Bellows and Short, 1994; Rasby et al., 1989).

Today's beef producers are still heavily reliant upon a natural mating system to impregnate breeding females in order to procure marketable calves. In fact, 90-95% of all newborn beef calves in Westernized agriculture are still conceived under natural mating conditions (Godfrey and Lunstra, 1989; NAHMS, 1997). In terms of impact on economic returns, Trenkle and Willham (1977) compared both heritability and heterosis of several traits among cattle breeds. Based on these comparisons, they found that reproductive performance of beef herds is approximately five times as important as growth rate of calves and ten times as important as quality of carcass end-products, with respect to yearly gross income receipts and based on present recommendations for bull to female ratios (Trenkle and Willham, 1977). Hence, it is axiomatic that the reproductive capabilities of breeding bulls in polygynous mating scenarios, under

present beef production goals, are a vital issue when considering herd profitability. Ironically, bulls' reproductive capabilities are not routinely assessed even though *Breeding Soundness Exams* are established as the baseline criteria for determining suitability of a particular bull as a breeding member of the herd. Such exams are aimed at evaluating sperm quality parameters, ejaculate properties, and basic physical soundness (Chenoweth, 1981). Reproductive behavior of bulls is not currently evaluated under the breeding soundness exam (Chenoweth, 1981), although most livestock producers are aware of the large variation in male sexual proficiency. When buying bulls for use in natural mating systems livestock producers seldom, if ever, have any estimate of a particular bull's copulatory proficiency (Boyd et al., 1989). The dynamic behavioral continuum within which male and female bovines interact has received sparse attention and the logistics of behavior research within this species can be difficult. Nevertheless, research in this area is needed and knowledge of factors that control the expression of sexual behavior within polygynous mating systems could lead to methods which enhance reproductive efficiency in beef cattle herds.

Throughout the remainder of this review of literature, I would like to explore alternative hypotheses to explain reproductive behavior of cattle. I utilize an interdisciplinary approach to investigate this topic with the intent of developing a novel theory about bovine sexual behavior. These views contradict prevailing hypotheses utilizing conventional methodology. Specifically, I am interested in exploring the possibility that presently accepted concepts of bull sexual behavior may be biased by certain culturally-based assumptions concerning the sexual roles of males and females. Through critical evaluation of these assumptions, development of an alternative theory concerning the dynamic mating continuum in which cattle may have evolved could be realized. In turn, this could lead to new testing paradigms and hypotheses, illuminating factors which govern the expression of bovine sexual behavior.

In the remainder of my dissertation, I describe in detail research which represents the first phase of a long-term research program that seeks to illuminate the physiological mechanisms controlling sexual behavior in cattle. My research was directed at

establishing a reliable and valid procedure for remotely assessing sexual behavior in bulls with the objective of using this procedure to evaluate the effects of female novelty and receptivity on the expression of sexual behavior in male bovine (Chapter 2). In addition, I repeatedly tested a group of bulls to determine if sexual behaviors vary among individuals and whether such behavior was repeatable within these individuals (Chapter 3). Finally, I compared sexual behavior of bulls that were either serially or group exposed to varying female stimulus conditions (Chapter 3). Results from these experiments served to confirm the test procedure which was based on determining its reliability and validity. These measurements would then constitute a quantitative description of sexual behavior when bulls are exposed to variable female stimulus conditions and add basic information regarding the expression of sexual behavior in the bovine.

Utilitarian Views of Bull Sexual Behavior

Based on the above assessment associated with overall beef herd fertility, the sexual behavior of bulls has been studied with the intent of developing theories which support methods that serve to predict the suitability of particular bulls as herd sires. Another common goal of conventional research in this area is aimed at reducing the time, labor, facilities, and cost associated with testing bull sexual behavior (Blockey, 1975; 1976 a,b; 1981a; Chenoweth, 1979; Price and Wallach, 1991 a,b,c). From the theories proposed by Blockey (1975), Chenoweth (1979), and Price (1987) came the development and adoption of practices which sought only to explain bull sexual behavior on the bases of its potential to impact profitability of beef cattle production. Hence, the hypotheses supporting the conventional approach to studying bull sexual behavior have not been fully tested in the light of an ethological approach to studying behavior. An ethological approach would embrace equal consideration of how male and female bovines interact sexually. As a result, there has been little critical evaluation of the fundamental assumptions associated with the supporting conclusions of the conventional methodology. It is often assumed, for example, that selection criteria developed from the conventional approach and used to hierarchically rank bulls can be employed as a

means to increase reproductive efficiency in beef herds. The selection criteria usually involves restraint and sedation of females in so-called “service stanchions” and hierarchically ranking bulls as to their ability to repeatedly copulate with the inanimate females (Blockey, 1975, 1976a,b,c; Chenoweth, 1981; Lunstra, 1986; Price and Wallach, 1991a,b,c). By selecting bulls based on their performance in such tests, it is assumed that producers could reduce the number of bulls needed to inseminate particular numbers of free-roaming, female cattle. Simply by employing such methodology, the reproductive efficiency of beef herds would be increased, as argued by Blockey (1975; 1976a,b,c). A quote from one of his articles published in an Australian veterinary journal in 1976 seems to epitomize this utilitarian view of bull sexual behavior.

“Despite the overwhelming predominance of natural mating in beef herds, no attempt has been made to measure the serving efficiency of bulls during pasture mating. It is probable that there is a marked between-bull variation in this characteristic. Should there be, it is possible that variation in serving efficiency can be exploited to increase the fertility of the cow herd and to reduce the number of bulls required for pasture mating. An important and potentially fertile field of research awaits investigation.”
(from Blockey, 1976a, pg. 390).

This utilitarian view is generally held among most researchers in the field of animal and (or) veterinary sciences. In part, embracing this utilitarian view reflects the applied nature of these disciplines. Nevertheless, this view ignores basic behavioral and ethological approaches to investigating the expression of behavior in animals. By ignoring ethological approaches to behavior, researchers have embraced methodology which disregards the involvement of female bovine in influencing males’ access to copulation; this research spans almost thirty years of publication (Blockey, 1976b; 1979; 1981a,b,c; Chenoweth et al., 1979; Christensen et al., 1982; Lunstra, 1980; 1986; Coulter and Kozub, 1989; Landeata-Hernandez et al., 2001; Bertram et al., 2002).

In my view, bulls are opportunistic breeders in that as adults, barring any sickness or other physical malaise, they are prepared to repeatedly copulate and inseminate

females should the opportunity arise. Bulls exhibit several phenotypic features that could facilitate repeated inseminations during a relatively short period of time (i.e. large testicles relative to body size, a fibroelastic penis that constantly remains in a semi-erect state, a relatively short postcopulatory refractory period, etc.). However, there are certainly limitations to this ability in terms of fertility and expression of behavior. In addition, estrual females are only receptive to copulation during a short period of time (i.e. estrus or “heat”) relative to the 21-day estrous cycle. In the beef female, estrus lasts only 12-18 hours, with a mean of 15 hours and a range of 6-24 hours (Senger, 1999). Interestingly, most reproductive physiology research in the field of animal science is aimed at increasing the reproductive efficiency of beef herds by focusing primarily on understanding and controlling the female estrous cycle. There is tremendous attention devoted to developing methodology aimed at decreasing age at first puberty, minimizing the postpartum anestrous interval, and manipulating ovarian structures with the final intent being induced, synchronous cyclicity in breeding females. This tendency by researchers to focus on control of and power over female reproduction reminded me of topics in a text written by Carolyn Merchant (1980) entitled *The Death of Nature*. Below, I attempt to provide a succinct description of some of the most salient points in her work and further attempt to interleave these concepts into our present discussion.

In this very thorough and complex work, Carolyn Merchant (1980) offered an elaboration on the interconnectedness between women, the scientific revolution and the ecology movement and painstakingly detailed two prevailing world-views, namely, those that are *mechanistic* versus those that are *organic*. A mechanistic view of nature refers to the relationship between humans and nature that supports the idea that plants, animals and other natural resources are valuable only to the extent to which they can be used and exploited by humans for humans (Zimmerman et al., 1993). Integral to the mechanistic view, and stemming directly from numerous ancient, (mostly Caucasian and male) philosophers, is the belief that the universe is divisible into simple particles and that all whole entities or forms are fundamentally made up of these particles and

nothing more. Different “wholes” (e.g. oceans, mountains, planets and air) are simply different configurations of these particles and are no more than the sum of these parts (Merchant, 1980). In addition to this *ontological assumption*, a *principle of identity* is also assumed in the mechanistic view such that the universe is assumed to have natural order and, thus, displays law-like behavior governed by rules (Merchant, 1980). Through scientific inquiry and reductionism (i.e. reducing explanations into their simplest form) nature and its laws are predictable (Merchant, 1980). The third assumption embraced by the mechanistic view posits that knowledge and information can be abstracted from this natural world and that this information is assumed to be *context independent* (Merchant, 1980). That is, a changing, imperfect nature could be described, predicted and controlled by science advocating rigid, limited, and restricted structural reality (Merchant, 1980).

Hence, a limited view of reality allows for the possibility of control whenever phenomena are predictable, regular, and subject to rules and laws (Merchant, 1980). Since information gleaned in this manner can be analyzed by evaluating the individual parts and manipulated by mathematics, a *methodological assumption* is also embraced (Merchant, 1980). Finally, an *epistemological assumption* is embraced in the mechanistic view wherein all sense data are discrete and not continuous; that is, we receive information about the natural world through our senses in minute particles of information (Merchant, 1980).

The mechanistic argument was founded mostly on a human’s ability to perceive these indivisible particles (i.e. atoms) and that they were identical and unchanging (Merchant, 1980). Thus, nature's wholes were simply sums of their parts and because particles were considered identical, this mechanistic view generally led to emphasizing quantification over qualification of characteristics. For example, mass, length, and velocity become fundamental concepts of reality, surpassing such "subjective" qualities like color, texture, odor, and taste (Merchant, 1980). This mechanistic view, posits Merchant (1980), was solidified by the philosophy and direct sociopolitical influence of Aristotle, Plato, and Renè Descartes, among others. It became thoroughly entrenched in

society during the Scientific Revolution by the influence of individuals such as Francis Bacon, Isaac Newton, William Harvey, John Locke, David Hume and Thomas Hobbs (Merchant, 1980). Merchant (1980) went on to thoroughly describe how these views and assumptions about the structure of being, knowledge and scientific method made possible human manipulation and control of nature, which, she argues, has had devastating impacts on our environment. Furthermore, her analysis revealed numerous instances where nature was wholly viewed as in the realm of women, who, for thousands of years, have been viewed as being more nurturing and unpredictable, akin to nature (Merchant, 1980). From Merchant's (1980) perspective, since women were so viewed, oppression of women in many societies is directly associated with the prevalence and widespread adoption of the mechanistic worldview toward nature (Merchant, 1980).

Carolyn Merchant would very likely suggest that the practices we utilize to control the bovine estrous cycle reinforce a mechanistic view of female sexuality. Specifically, Merchant (1980) wrote that order and power are integral parts of the mechanistic view of nature and provides primary impetus for justifying actions taken by humans against nature solely for the good of humans. In general, the conventional approach to studying bull sexual behavior embraces these specific assumptions and further accepts certain cultural biases about the sexual roles of males and females in the mating process. Conventional methodology seems to be focused on an assumption that bulls are "active" and powerful while female bovine are "passive" and weak in the reproductive process. These views, of course, are not uncommon. The active-male/passive-female dualism has been pervasive in Western culture for the past 2000 years, yet, are associated only with a mechanical perception of reality (Merchant, 1980). While respecting the purpose of the applied nature of animal science, I believe that these androcentric views about bull sexual behavior interfere with our understanding of the sexual interplay between male and female bovines. In my opinion, there is an appreciable need for understanding the intricacies of how males and females interact in ways that ultimately affect reproductive efficiency of beef cattle herds.

Merchant (1980) and other ecofeminists suggest that we reconsider the organic view of nature. With respect to research in bull sexual behavior, this might entail equal consideration of not only the interactions between males and females, but consideration of the broader context of these behaviors within an ecological framework. Perhaps a step in that direction could be an ethological approach, exemplified by the research of Konrad Lorenz, Nikolaas Tinbergen, and Karl von Frisch. Ethology is largely concerned with the behavior of organisms as expressed in their natural environment (Lehner, 1998). In addition, the field of ethology, which originated in Europe, sought to investigate genetic and evolutionary underpinnings of behavior, and, thus, embraced the notion that an animal's behavior has both innate and genetic bases. Most ethologists suggest that their work falls within the four categories of investigation suggested by Tinbergen (1963). Specifically, function, causation (i.e. mechanism), ontogeny and evolution (e.g. phylogenetics). Questions regarding the function of behaviors are related to both proximate function (e.g. immediate consequences of a behavior on the individual, group, or environment) and ultimate function (e.g. adaptive significance of a behavior with respect to improving fitness). Causation questions are related to the underlying mechanisms that govern the expression of behavior (e.g. endogenous and exogenous stimuli eliciting a response that can be either conditioned or not). The ontogeny of a behavior refers to the development of the behavior within the lifetime of the individual whereas questions regarding the evolution of behavior refer to the developmental processes at work at the level of the species.

Another large group of scientists were also concerned with the study of animal behavior, but the focus for this research was on model organisms (e.g., rats, pigeons, mice) in a controlled laboratory setting and was aimed at answering the mechanistic underpinnings of behavior (i.e. behaviorism). The classic works by B. F. Skinner led to the development of the use of learning paradigms and the infamous Skinner Box. A popular tenet embraced by behaviorists viewed behaviors as largely the product of the environment. Hence, differences between ethology and behaviorism led to a debate on the causes of behavior and are epitomized in the phrase "nature versus nurture".

Perhaps the answer to this debate lies not in terms of either genes or the environment, rather the development of behavior results from a more complex interaction between genes and the environment.

The field of behavioral ecology would appear to be a most germane field of study in terms of finding convergence in this debate and lends appreciable possibility for an organic approach to studying sexual behavior in the bull. Behavioral ecology is a broad based discipline that utilizes both empirical and theoretical approaches which endeavor to understand the whole range of behaving organisms. Behavioral ecology specifically endeavors to include 1) the use of ecological and evolutionary processes to explain the occurrence and adaptive significance of behavior patterns, 2) the use of behavioral processes to predict ecological patterns, and 3) empirical, comparative analyses relating behavior to the environments in which they occur (Lehner, 1998). Although well beyond the scope of my dissertation work, which was aimed at developing an ethological approach to studying behavior in the bovine, future researchers interested in sexual behavior in this species might do well to collaborate with behavioral ecologists who have provided considerable insight into methods aimed at studying behavior at the level of genes, ecology, physiology, development and learning, evolution, and sociality. Embracing the field of behavioral ecology would provide novel schema for understanding sexual behavior in the bovine and aid in illuminating the process of adaptation in behaviors at a variety of temporal scales, which is currently understudied in the discipline of animal science.

On the Ambiguity of Conventional Terminology

Many reviewers and researchers (Blockey, 1975; 1976a,b;1979; 1981a,b,c; Chenoweth, 1981; 1982; Price, 1987; Godfrey and Lunstra, 1989; Bertram et al., 2002) use the term *service* to describe male copulation in the bovine. Perhaps the term is used in a manner that confounds our ability to understand sexual behavior from both the male and female perspectives. The term *service* with respect to bovine reproduction was defined by Sembraus (1971) (translated and cited by Blockey, 1975; 1976a) as a motor pattern that results in the male lifting his forequarters off the ground, clasping the female's

pelvis, and bringing the tip of the erect and protruding penis near the vaginal orifice. After minor postural adjustments, the protruding penis penetrates the vaginal orifice, resulting in a lengthening of the penis (due to relaxation of the penis retractor muscle and straightening of the sigmoid flexure) followed by one or more intromissions leading to ejaculation (Blockey, 1975; 1976a). During ejaculation, the male will often display a final, deep pelvic thrust which at times lifts his hindquarters completely off the ground (Blockey, 1975; 1976a).

The term *Serving Capacity* was originally used as a measure of the number of these “services” achieved by bulls of unknown social status during 7.5 hours of group pasture interaction with ovariectomized females who received a single injection of an estradiol analogue to induce estrus behavior (Blockey, 1976a). Hence, “serving” has been readily used to describe a set of behavioral events culminating in male ejaculation inside a female’s vagina (i.e. an interaction between the male and female). Ejaculation, under these circumstances, is assumed to have occurred when visually verified by a final, deep pelvic thrust followed by withdrawal of a fully erect penis from the vagina (Sambraus, 1971, cited and translated by Blockey, 1975; 1976a).

This term is ambiguous for a number of reasons. Males can ejaculate without a deep, final pelvic thrust when intromitting with a female; at times, they may even ejaculate without intromission (personal observation). Most of researchers who readily use the term “service” have not actually verified that an ejaculation took place (i.e. verified that ejaculate was expelled from the penis) nor can they account for those instances where a bull intromits and ejaculates without a final, deep pelvic thrust. This would undoubtedly have an effect on a bull’s “serving capacity” and would likely influence female conception rates. Furthermore, the expression of this behavior and its related physical properties, with the exception of possession of the intromittant organ by the male, may not be exclusively controlled by the male.

Questions arise regarding the use of the term “serving capacity”. Do females have their own “serving capacity” in terms of placing themselves in juxtaposition to the male? Can the female “service” the male by placing herself in ways that would

maximize probability of copulation? If so, do females have a propensity for doing this with multiple males? When a male and a female copulate, aren't they "servicing" each other? The use of this term in the literature promotes the assumption that the active, powerful bull simply roams around the pasture and "services" females, who are assumed to be merely homogeneous, inanimate objects (i.e. passive and weak) or, as described by Price (1987), inverted, "U-shaped" objects. The more times and faster the bull does this, the higher his "serving capacity" regardless of female interaction. In my view, this term virtually ignores the fact that when a male and a female are copulating, they are both exhibiting equally complex behaviors, especially when one considers the behaviors that brought them together in the first place. Additional complexity arises when one considers the possibility that sexual behavior between male and female bovine during natural mating scenarios could intricately oscillate between periods of sexual activity and quiescence.

Embracing the conventional meaning of "service" fails to recognize the sexual continuum within which males and females in this species interact and supports a theoretical framework that seems inconsistent with the way males and females interact during sexual encounters. I will not use the term "service" in this dissertation to describe bovine copulatory behavior because 1) it is ambiguous and 2) it fails to adequately inform us about the mating behavior of the female and suggests female passivity within the context of mating behavior. A recurring theme throughout my dissertation will advocate debunking the myth of the passive female. Accordingly, I will continually use the words, *copulate* or, where specifically referring to the act of penis insertion into the female's vagina, *intromission* in place of "service" or "serving". Two exceptions to my using this term will be 1) when citing other literature directly and 2) in a forthcoming section on development of the so-called "Serving Capacity Test" and its variants. Under these circumstances, I will enclose the term(s) in quotations to note their vernacular usage.

Ontogeny of Sexual Behavior in the Male Bovine

The *ontogeny* of behavior refers to the process by which particular behaviors develop within the lifetime of an individual. More specifically, what internal and external factors influence the way in which behavior develops during the lifetime of the individual (Martin and Bateson, 1993). Although the entire repertoire of sexual behavior of bulls has been described thoroughly in several reviews (Wierzbowski, 1966; Simbraus, 1971; Blockey, 1976a; Chenoweth, 1981; 1983; Price, 1987), there has been a consistent tendency by reviewers to insist that bull sexual behavior is reducible to only two major aspects; namely libido (sex drive) and mating ability (physical ability to copulate) (Blockey, 1976a; Chenoweth, 1983; Lunstra, 1986). It is often suggested that male's possess an *innate* sexual drive (Chenoweth, 1981; Price, 1987). As noted in the previous section, this view supports the questionable notion that sex drive has little to do with females. It is well known that sexually immature bull calves will express basic patterns of sexual behavior (i.e., mounting) which lends credibility to the suggestion that at least some sexual behaviors are innate (Lesmeister and Ellington, 1977). Bouissou (1975) reported that mounting activity occurred far in advance of puberty, ejaculatory competency and that the majority of mounting activity eventually was of a rear-mounting orientation. Bouissou (1975) further suggested that both heterosexual and homosexual mounting occur at a very young age in bull calves and may be accompanied by adult-like pelvic thrusting. It is also well established, however, that immature bull calves can not intromit or ejaculate readily until they reach full sexual maturity; in fact, physical separation of the penis from the preputial sheath does not occur until 8-10 months of age (Ashdown and Pearson, 1973). Hence, the behavioral pattern of mounting and thrusting in the male bovine may be innate but whether or not this is indeed innate sex drive is conjecture. It seems clear, however, that the physical means to carry out adult sexual motivation does not develop until final sexual maturation.

Full expression of sexual interest and mating behavior requires coordination of behaviors with the context of mating and several researchers have alluded to a *learning*

component of sexual behavior in the bull. Couttie and Hunter (1956) suggested that when young bulls were reared in isolation, many failed to respond or showed less interest in mounting when first exposed to estrual females compared to bulls raised with females. Conversely, Bouissou (1975) suggested that males reared in complete isolation often will eventually exhibit normal mating behavior when exposed to estrual females. Lunstra (1986) suggested that young, inexperienced bulls must undergo a “learning process” and (or) “acclimation” with females and behavior testing paradigms before they exhibit stable reproductive behaviors, although he failed to elaborate on what this learning process entails. Other studies have found that rearing young bulls with females did not improve their sexual performance as adults compared to similar aged males not reared with females (Lane et al., 1983). As Chenoweth (1982) suggested, the degree to which learning impacts the ontogeny of sexual behavior in the bull varies in different studies from negligible to significant. Price (1987) further stated that most young, sexually naïve males, regardless of species, are almost always inept upon first exposure to estrual females; after continued exposure many go on to eventually mate, suggesting that experience likely influences the ontogeny of sexual behavior in a somewhat acute manner. It was not clear from these studies if mounting behavior itself, or the accompanying tactile stimulation of the penis, or both, provide important information to the developing bull. A study conducted in 1986 sought to investigate this very issue.

Katz and Price (1986) provide the most complete information to date on the role of penile stimulation on the ontogeny of reproductive behavior in the bull. Katz and Price (1986) were interested in determining the role of afferent neural input from the penis with or without copulatory experience on the ontogeny of reproductive behaviors in the bull and devised four experimental treatments to help answer their research questions. The four treatments were 1) control, 2) surgical deviation of the penis (which prevents intromission), 3) penile neurectomy (severing efferent and afferent neural connections to the penis), or 4) penile deviation plus neurectomy. Using restrained and unrestrained teaser females, bull sexual behavior tests were conducted at three-month

intervals from 9-24 months of age. As one would expect, intact control bulls had the highest copulation frequency (i.e. number of copulations•bull⁻¹•40-minute test⁻¹); there were no observed copulations in bulls that received surgical penile deviation. Interestingly, 4 of 13 neurectomized bulls attained the ability to copulate. Bulls with surgically deflected yet neurally intact penes mounted more frequently compared to the bulls in all other treatments (Katz and Price, 1986). However, control bulls also exhibited low mounting response, similar to that of bulls in both groups of neurectomized bulls. According to Katz and Price (1986) this likely occurred as an artifact of the postejaculatory interval, in which bulls showed no sexual behaviors for a limited time after copulation. By placing patches over female vulvae (i.e. a practice that also precludes intromission), Katz and Price (1986) demonstrated that control bulls showed a dramatic increase in mounting frequency, comparable to that of the deviated, neurally intact bulls. There were lower levels of mounting activity expressed by both groups of neurectomized bulls and this was believed to be caused by the lack of facilitative sensory input from the penis (Katz and Price, 1986) or the combination of penis deflection and neurectomy.

Katz and Price (1986) concluded from this study that copulatory experience is not essential to the development and maintenance of mounting behavior in the bull but sensory stimulation from the penis certainly facilitates its expression (Katz and Price, 1986). Perhaps another explanation for the data from Katz and Price (1986) is that bulls that can not intromit and ejaculate mount more often because the unrestrained, estrous females allowed them to. Katz and Price (1986) alluded to this possibility by suggesting that unrestrained females displayed intermittent periods of unwillingness to stand for mounting, despite their estrual state; this resulted in a higher mounting frequency when females were restrained. It was clear in the Katz and Price (1986) study, however, that the inability to ejaculate or intromit, even when bulls were provided unlimited access to females, did not completely inhibit their mounting activity although there was marked attenuation. Based on these observations, it is possible that intromission and(or) ejaculation by the male induces sexual refractoriness in females.

Many questions remain in my mind about these concepts. What exactly do calves learn about sexual arousal, copulation, and sexual gratification? What role could conditional learning play in this process? Based on the above contradictions and limited inquiry into these phenomena, it seems that further studies are needed to determine the ontogeny of sexual behavior in both the male and female bovine. From a behavioral ontogeny standpoint, the development of these experiences is likely mediated by the context and consequences of the expression of mating behaviors. For either a female or male calf, mounting other males or females who are not receptive to mounting, would certainly provide experience with consequences and perhaps would provide important reinforcement on the context of the expression of the behavior. If the mounted individual is motivated to allow mounting, this, too, would provide some experience with context and consequences. Upon acquisition of sexual maturity perhaps both sexes express innate, rudimentary motor patterns associated with mounting and pelvic thrusting but learn additional, differential context as they encounter receptive partners. As we shall see, mounting, from both the female and male perspective, will become immensely important for establishing a successful copulation and the postejaculatory interval provides an important feedback mechanism that likely helps modulate resumption of sexual behaviors during the postconsummatory phase.

The Dualism of Bull Libido and Sexual Performance

In the previous section, I suggested that various factors influence the rate and extent to which reproductive behavior events become coordinated with the context of mating within the lifetime of an individual (i.e. ontogeny of sexual behavior). As previously suggested, raising prepuberal bulls in all-male groups could negatively influence putative learning components of heterosexual behaviors and negatively influence adult libido (Chenoweth, 1981; 1982; Price, 1987). There has been little, if any, mention in the literature as to the possibility that the female bovine also exhibits both innate and learned sexual behaviors. In fact, the term *libido* is used primarily to describe a trait possessed solely by males (Chenoweth, 1981). For example, a definition from the

Chenoweth paper (1981, pg. 155) indicates that libido is, “the willingness and eagerness of a *male* animal to mount and to attempt service of a female.” (emphasis added). One could construe, perhaps erroneously, that females do not possess libido. These appear to be examples of a type of dualism that is readily evident in the scientific literature available on this topic. The term *dualism* was originally used by the philosopher Thomas Hyde around the beginning of the eighteenth century (Merchant, 1980). Dualism, he suggested, was the idea that the world is made up of two and only two elemental categories which are incommensurable or mutually exclusive. This includes distinctions commonly made between mind and body, good and evil, universal and particular, objective and subjective, and male and female. In westernized cultures, it is common to suggest that the former terms in each dualism are superior to the latter terms (e.g. the mind is superior to the body, etc.; Merchant, 1980). The dualism of libido and sexual performance embraces the view that these factors are mutually exclusive; furthermore, it seems these concepts are not readily used to describe female sexual behaviors.

In contrast to dualism, two other philosophical positions concerned with the number of substances or worldviews are *monism* and *pluralism* (Merchant, 1980). Monism is the view that there is only one elemental factor in which to view the world whereas pluralism maintains that there are many things which constitute our worldviews. It is within this context, specifically associated with the bovine, that I advocate consideration of *male libido* as the willingness and eagerness of the male to mount and complete copulation with a female, whereas *male mating ability* refers to particular physical behaviors associated with penis extension and intromission (i.e. inserting the penis into the vagina preceded by thrusting, etc.). We can also hypothesize that *female libido* exists and refers to the willingness and eagerness of the females to seek out mates and allow mounting (either heterosexual or homosexual) and intromission by the male(s). Perhaps we could further hypothesize that *female mating ability* refers to her ability to exhibit postural adaptations and visceromotor responses that would allow repeated mounting and intromissions.

Apparently, the need to categorically differentiate libido from mating ability is an attempt at distinguishing between behaviors that are related to motivation and those that are related to execution of specific motor patterns resulting from this motivation (i.e. performance). Again, these concepts seem to embrace dualisms that serve to inform our thinking but affect only our perceptions of a mechanical reality. In my view, these terms seem to be more closely related to ethological descriptions of sexual behaviors as being either *appetitive* or *consummatory* which further embrace the notion of equality between the male and female. Meisel and Sachs (1994) reached similar conclusions. In fact, they (Meisel and Sachs, 1994) go on to state that the terms “libido”, “performance” and “potency” are not readily used in scientific discourse associated with human and nonhuman male sexual behavior. On the contrary, almost every published researcher interested in bovine sexual behavior uses these terms to describe, in dualistic terms, differences between motivation and performance (Blockey, 1979; Price, 1981; 1987; Chenoweth, 1981; Lunstra, 1986). These dualisms seem to raise questions of 1) whether the expression of certain sexual behaviors is learned or innate and 2) whether they are sexually dimorphic. As I previously stated, terms such as libido and performance are consistently used for describing only male sexual behaviors (Blockey, 1979; Chenoweth, 1981; 1987; Lunstra, 1986) and fail to inform us about female sexual behavior.

In the following section, I provide a detailed description of the sexual behavior of cattle using an ethological approach. As Meisel and Sachs (1994) suggested, neither an androcentric nor a gynocentric perspective of sexual behavior will suffice in completely describing this complex, multifactorial process and I embrace that contention with specific reference to the bovine. Hence, my goal in this section is to describe bovine sexual behavior as highly interactive, requiring the perspectives of both the male and the female.

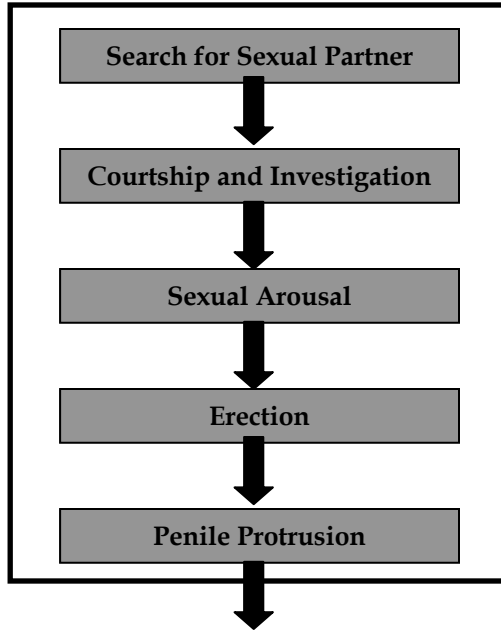
Basic Descriptions of Bovine Sexual Behavior

It is commonly accepted (Chenoweth, 1981; Price, 1987; Senger, 1999) that the entire gamut of reproductive behaviors of cattle can be hierarchically and linearly defined,

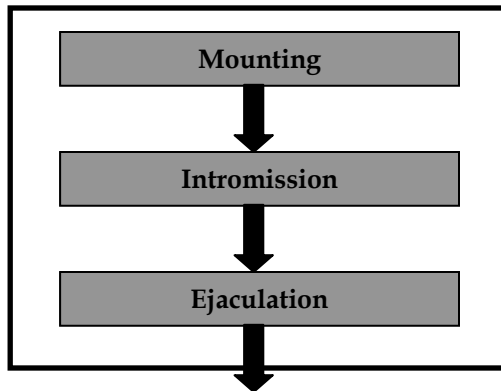
depending upon when particular behaviors occur relative to one copulation (i.e. precopulatory, copulatory, and postcopulatory behaviors). In a popular reproductive physiology text specifically geared toward study of farm animals, Senger (1999) suggests that reproductive behaviors occur in these three distinct stages. Figure 1 from the Senger (1999) text outlines the events within these stages. As one can see, this is a hierarchical view because different sexual behaviors fall into strict, temporal stages relative to copulation. Under the hierarchical view, for example, flehmen responses do not occur outside of the stage of precopulatory behaviors. This view is linear because one stage strictly follows another which is strictly followed by the next. There are no feedback systems in place which would allow us to further conceptualize resumption of sexual activity following one copulatory event. It is important to point out that the terms precopulatory, copulatory, and postcopulatory are 1) absolutely focused on the act of copulation and 2) almost exclusively detail only male sexual behaviors and do not equally consider female sexual behaviors within each stage. Hence, this model also embraces a conventional, androcentric view of sexual behavior.

Should we continue to embrace these views? On the one hand, copulation represents only one, minute part of a multifaceted, interactive exchange between the male and female. Researchers who have embraced the hierarchical, linearized construct (Chenoweth, 1981; Price, 1987; Senger, 1999) fail to acknowledge that female bovine display copulatory behaviors. While the hierarchical and linearized view certainly informs our thinking by providing a simplistic concept of reproductive behavior, it is important to realize that sexual behavior, as with most behaviors, can occur sporadically and outside the bounds of these abstract, mental constructs. Furthermore, this model fails to account for behavioral plasticity and seems overly focused on the male. For example, a precopulatory event (e.g. grooming, flehmen response, etc.) could actually occur directly after copulation (i.e. during the postcopulatory phase). In the bovine, as in many rodents, copulations occur in distinct bouts of mating, resulting in an oscillating pattern of behavioral expression. This is most likely due to some sort of

Precopulatory Behavior



Copulatory Behavior



Postcopulatory Behavior

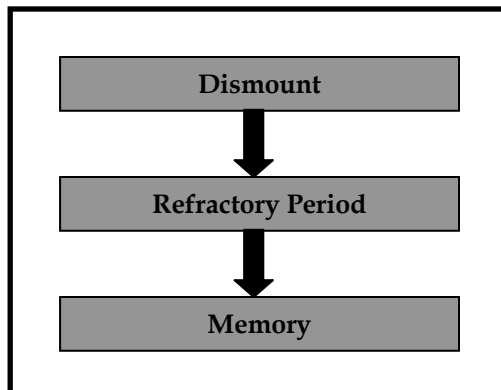


Figure 1. The hierarchical, linearized view of bovine sexual behavior taken from Senger (1999). During the precopulatory stage, searching for a sexual partner leads directly to courtship, sexual arousal, erection and penile protrusion, in that strict order. During the copulatory stage, mounting occurs followed by intromission and ejaculation. Finally, during the postcopulatory stage, the male dismounts and becomes refractory to other sexual behavior; mating experiences may impart both positive and negative reinforcements which somehow develop into memory in the male. As one can see, this is a hierarchical view because different sexual behaviors fall into strict, temporal stages relative to copulation. Under the hierarchical view, for example, flehmen responses do not occur outside of the stage of precopulatory behaviors. This view is linear because one stage strictly follows another which is strictly followed by the next one and so on. There are no feedback systems in place which would allow us to further conceptualize resumption of sexual activity following one copulatory event.

feedback mechanism(s) involving interactions between the male and the female. The hierarchical, linearized view does not allow us to see this. A more complete and thorough description of reproductive behavior in cattle is needed. Beach (1976) believed that the mating process involves dyadic, heterosexual mating patterns wherein each participant is equally involved and that there are feedback mechanisms governing behavioral plasticity. Critical evaluation of research dealing specifically with bovine sexual behavior utilizing these fundamental concepts requires that I examine this process from the perspective of a discipline outside of animal science. The ethological concepts of appetitive and consummatory sexual behaviors appear useful in this regard.

Ethological Descriptions of Appetitive and Consummatory Sexual Behaviors

Behavior that denotes sexual excitement and arousal are considered appetitive behaviors whereas consummatory behaviors are directly involved with the copulatory response (Beach, 1976). Early work from ethologists and experimental psychologists described appetitive (both anticipatory and preparatory) behaviors as those which are exhibited in a manner that changes the spatiotemporal relationship between the animal and incentive stimulus (Pfaus, 1996) and serve to bring an individual displaying the behaviors into contact with the incentive stimulus (i.e. the partner). Consummatory behaviors, it follows, would be those behaviors performed once physical contact is established between the animal and the incentive stimulus (Pfaus, 1996).

For the consideration of appetitive and consummatory phases of sexual behavior, I rely heavily upon the work of Pfaus (1996) who advocated conceiving of such with the use of overlapping Venn diagrams in which the overlap area defines criteria for behaviors that may occur in both phases. In addition to the concepts proposed by Pfaus (1999), I also include work by Beach (1976) who provided insight into how appetitive and consummatory behaviors are reciprocating and oscillating between and within mating partners, respectively. Figure 2 was constructed with the intent of developing a conceptualization that includes both of these authors' ideas. I have intermingled and modified the diagrams to include relevant behaviors that are specifically notable in the

bovine. In the next section, I elaborate on Pfaus' (1999) recommendation that we subdivide certain behaviors that may be influenced by sexual experience, learning, and conditioning.

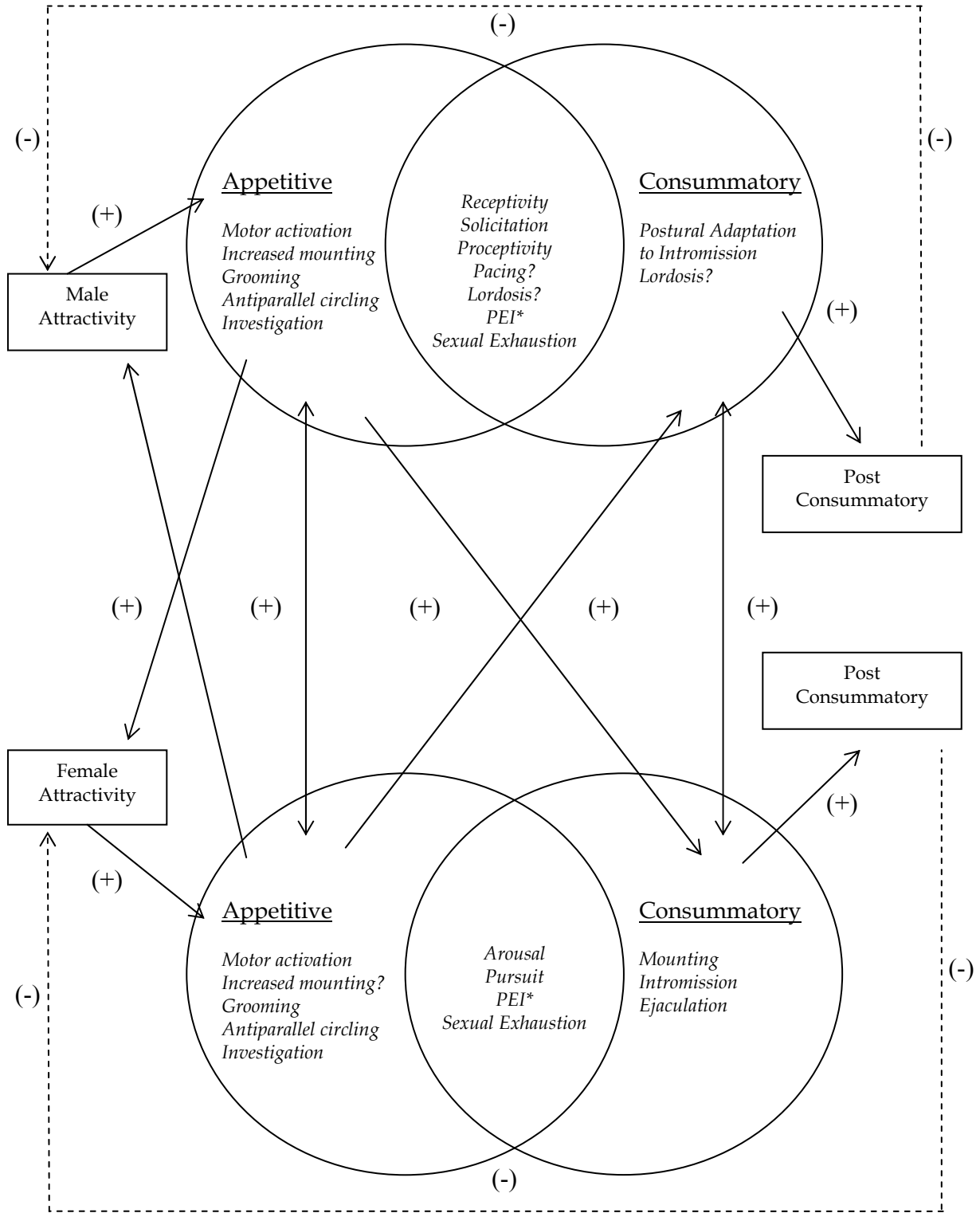
Subdivisions of Reciprocal Mating – Anticipatory and Preparatory Behaviors

Pfaus (1996) further suggested that we should subdivide behaviors comprising the interface between appetitive and consummatory behaviors (Figure 2) as either *anticipatory* or *preparatory* (Figure 3). Under these concepts, both anticipatory and preparatory responses are exhibited in anticipation of the primary incentive (i.e. the conspecific partners; Pfaus, 1996). The distinction is that anticipatory responses are not necessary to obtain [the primary incentive] whereas preparatory responses *must* be made to obtain it (Pfaus, 1996). The possibility exists that both types of these behaviors are learned and, if so, likely influence full expression of sexual interest and mating behavior in the bovine, which requires coordination of behaviors within the context of mating. Below, I elaborate more precisely on these responses.

Anticipatory Responses

Anticipatory responses include those behaviors that are conditional upon sexual excitement initiated by partner attractivity but are not required to obtain the primary incentive. These responses could include locomotion, investigation, grooming, and various other adjunctive behaviors (Pfaus, 1996). Note, once again, that most appetitive behaviors are not sexually dimorphic in the bovine (see Figure 2). However, this certainly should not be construed to mean that there are no sexually dimorphic *anticipatory* behaviors in the bovine (Figure 3). For example, in a study by Geary et al. (1992) pre-ejaculatory emissions were readily noted and quantified even though bulls could not gain physical contact with the females. These sexually experienced bulls had pre-ejaculatory emissions more frequently when adjacent to estrual females mounting than when adjacent to diestrus females; frequencies of pre-ejaculatory emissions were similar when bulls were adjacent to either lone estrual females or estrual females mounting. Consider the general case of the sexually experienced bull visually observing female appetitive behaviors (e.g. homosexual mounting). Since he has had

Female Bovine

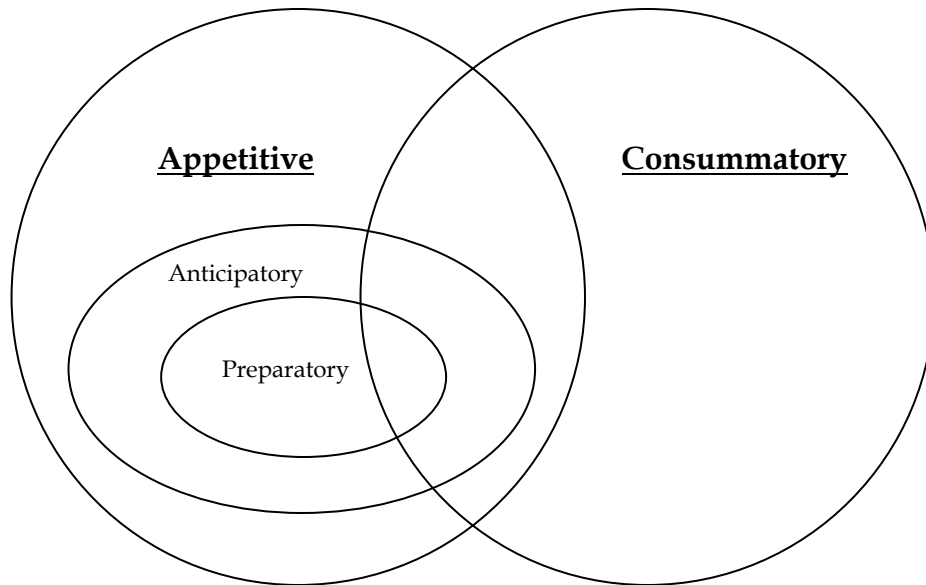


*PEI - postejaculatory interval

Male Bovine

Figure 2. Reciprocity in heterosexual mating in the bovine, adapted from models proposed by Pfaus (1996) (*Incentive Sequence Model*) and Beach (1976). Consummatory and appetitive behaviors are conceived of as two overlapping Venn diagrams in which the behavioral stream moves from left to right, that is, from appetitive to consummatory phases (Pfaus, 1996). The overlapping area emphasizes that the division between appetitive and consummatory phases is not fixed and some behaviors can modulate the transition between these phases. The overlapping area contains those behaviors that are displayed after contact between the partners has been made. Conspecific attractivity stimulates appetitive behavior which enhances the attractivity of the partner and elicits reciprocal appetitive behaviors. Reciprocal appetitive behaviors evoke consummatory behaviors. Execution of consummatory behavior provides feedback stimuli, inducing variable postconsummatory responses which are associated with decreased responsiveness to the incentive stimuli. This responsiveness was initially perceived as and induced by sexual attractivity of the partner. Notice how common elements of appetitive behaviors diverge into sexually dimorphic responses during consummatory phases of behavior (Pfaus, 1996).

Pfaus' (1999) Incentive Sequence Model - Anticipatory/Preparatory Distinction



Proposed for the Bovine

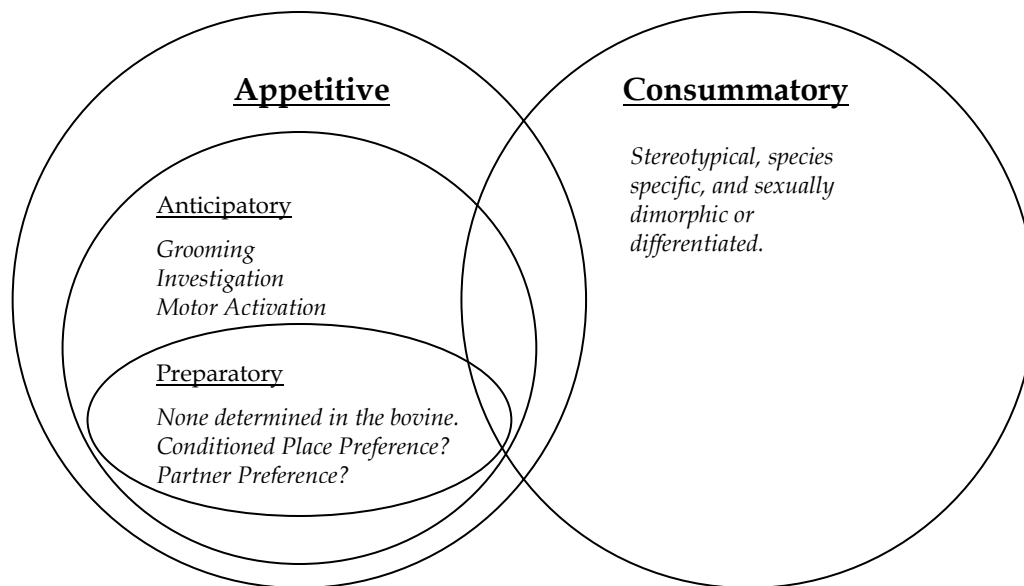


Figure 3. Distinction between anticipatory and preparatory behaviors (from Pfaus, 1996). Preparatory behaviors can be learned responses that animals must exhibit to acquire access to the stimulus partner (e.g. pursuit). Anticipatory behaviors may also be learned and occur in anticipation of the incentive but are not absolutely required to gain proximity to the stimulus partner. For example, in the sexually experienced bull, penis extension and pre-ejaculatory emissions when physical, but not visual, contact with stimulus females is precluded (see Geary and Reeves, 1992). Some appetitive behaviors are not learned and are, instead, instinctual or innate (e.g. unconditioned mounting, perineal or genital investigation, etc.). Behavioral plasticity is common among appetitive behaviors which are, thus, more flexible than consummatory behaviors. Consummatory behaviors are stereotypical, species-specific, and sexually dimorphic (e.g. male intromission, female lordosis, etc.).

some experience with coordinated sexual context, he would have learned to associate mounting females with eventual copulation. Hence, examples of learned, anticipatory sexually dimorphic responses might include precopulatory extension of the penis (personal observation) and (or) pre-ejaculatory seminal emissions from experienced bulls observing conspecific sexual activity (Geary and Reeves, 1992). It is difficult to elaborate on these same phenomena in sexually experienced female bovine. Although highly speculative, I would hypothesize that increased vaginal lubrication and clitoral engorgement in relation to sexual context could be learned, anticipatory responses in the sexually experienced female.

Preparatory Responses

There have been numerous published reports of learned, preparatory responses associated with rodent sexual behavior. Examples include, operant bar-pressing (Beck, 1986; Matthews et al., 1997), where the animal learns to press a bar to gain access to a sexual partner. In addition, female rats will cross an electrified grid to gain access to sexual partners (Myerson et al., 1973). More recently, researchers have utilized *Conditioned Place Preference* models to explore preparatory responses. Conditioned place preference is usually demonstrated by utilizing an experimental apparatus with connected but distinct chambers. Initially, each chamber is partitioned, and paired differentially with an unconditioned stimulus (e.g. sexual partner in one, control manipulation in the other). Upon test situations, the subject is allowed free access to each chamber and a conditioned place preference is said to have occurred if the subject spends more time in the reward-paired chamber (Pfaus, 1996). As of today, there have been no investigations into bovine sexual behavior utilizing these ethological paradigms.

When applying the model advocated in Figure 2 to the bovine, one could hypothesize that mounting is sexually dimorphic with respect to being consummatory and appetitive. Females express mounting appetitively (e.g. to change the spatiotemporal relationship between them and potential sexual partners) and not as part of the consummatory phase (i.e. females remain on the ground during the

consummatory phase). One could also hypothesize that bulls express heterosexual mounting only as part of their consummatory behavior. It is possible, however, that an additive effect of heterosexual mounting could occur through attracting other females to the partners mating. In this instance, we would consider this an appetitive behavior displayed by the male to attract other potential females to the area. Of course, in a pasture mating scenario with several bulls, such behavior could also attract other males, leading to conflict and perhaps a decrease in sexual activity. On the other hand, Blockey (1981b) demonstrated that bulls showed increased copulatory frequency with restrained, nonestral females after observing other males engaged in mounting activity. In 6 hour behavior tests at pasture, utilizing unrestrained, estrual females, higher mounting activity was displayed by bulls in double-bull tests (i.e. when 2 bulls were tested with 30 estrual females) than when bulls were tested singly. In each of these studies, there was no discussion as to the possibility that consummatory behaviors expressed by the male could have elicited more appetitive behaviors in conspecific females, resulting in greater, ensuing mounting activity.

The point I am trying to make here is that appropriate behavioral testing methodologies are necessary for evaluating the incentive or motivational responses associated with sexual behavior. To my knowledge, these methodologies (e.g. conditioned place preference, etc.) have never been employed in experiments using the bovine as a model. It would be interesting to determine the threshold of motivation to access stimulus incentives in both the male and the female bovine. Poor distribution of beef cattle in the Western United States has created a multitude of problems for cattle producers, resulting in disproportionate use of native ranges and increased feed costs (Vallentine, 1990). In situations where terrain and distribution of females is extensive, consideration of how breeding partners change their spatiotemporal relationship through partner attractivity seems a germane line of questioning. The interaction between male/male competition for females and whether females display a preference for dominant males warrants further consideration as potential factors governing beef herd fertility. In the next section, I continue with Beach's (1976) distinction among

attractivity, proceptivity, and receptivity and attempt to specifically adapt these concepts for consideration of the bovine and elaborate on how these concepts might further our understanding of bovine sexual behavior.

The Bases of Stimulus Attractivity

As we can see from Figures 1 and 2, consideration of and distinction among female attractivity, proceptivity, and receptivity is necessary. Female attractivity, according to Beach (1976), can be inferred from observations of behaviors exhibited by males toward the female. Execution of these behaviors is related to different forms of stimuli provided by the female including both behavioral and nonbehavioral cues. Beach (1976) provides an example that male appetitive behavior, such as approach and investigation, is dependent upon processing of exteroceptive stimuli, primarily through vision and olfaction in the bull.

When cycling females are in herds, and upon the attainment of estrus, they typically form small, sexually active groups consisting of females that are either in proestrus or estrus (Williamson et al., 1972). The behavioral oscillations that females exhibit after formation of the sexually active group involve head-butting, grooming, chin resting, repeated mounting and attempted mounts; some individuals stand firm to mounting. Hence, this period of the estrous cycle is characterized by states of heightened female sexual interest and homosexual mounting, both of which, in my view, exemplify the appetitive behaviors of female bovines (i.e. behavioral stimuli that are directly associated with bringing the female closer to the male).

To my knowledge, some researchers in animal science have failed to consider the possibility that these behaviors are appetitive in the female bovine. For example, the use of restrained females to quantify sexual behavior of bulls suggests that many investigators ignore or reject the notion of female appetitive behaviors (Blockey, 1975; 1976a,b; 1979; 1981a,b,c; Chenoweth et al., 1979; Lunstra, 1980; 1986; Christensen et al., 1982; Coulter and Kozub, 1989; Landeata-Hernandez et al., 2001; Bertram et al., 2002). The assumption has generally been that females' mounting of one another simply provides passive, visual cues to the bulls that, in their perpetually active roles, take it

upon themselves, due to their libido, to investigate the females. Blockey (1976a) went even further with the “powerful male” notion when he suggested that once a bull determines a cow is estrual, the bull induces the female to “stand quietly for service”. An alternative explanation is that females actively engage in mounting activity to increase their own attractiveness and maintain close proximity to the male(s) thereby increasing their own chances for successful copulation.

Senger (1999) claimed that another possible theory explaining female homosexual mounting behavior involves artificial selection by humans for female mounting behavior. Senger (1999) claimed that peasant farmers in medieval times could not afford to keep bulls, which were owned by wealthy, feudal land owners who controlled the breeding of cattle on their lands. Bulls were sequestered from the breeding females and peasants may have sought the use of bulls strategically (i.e. only when females were observed in estrus). Senger (1999) claimed that only those females that showed intense estrus (i.e. homosexual mounting) were kept for breeding and, thus, expression of female mounting behavior may have been inadvertently selected for by humans. This theory does not address, however, whether or not females express mounting in an appetitive fashion. In addition, there seems to be little doubt that certain behavior patterns are inherited, which has been one of the most important contributions to the study of evolution (Maynard Smith, 1982). However, genetically determined responses or behaviors are subject to the pressures of natural selection more predominantly than small influences caused by artificial selection (Maynard Smith, 1982). Feudal agricultural practices likely had little effect on overall, population allelic frequencies in genes associated with controlling sexual behavior in the bovine. One would need access to extensive sexual behavior research on cattle herds that have received no artificial selection by humans over long periods of time to evaluate this theory further. I can find no such information.

Female ungulates in estrus have been observed soliciting and pursuing males. For example, estrous ewes also form sexually active groups and seek out the ram(s) (Lindsay and Fletcher, 1972). In one study, (Lindsay and Robinson, 1961) a ram was

tethered in a large field and at the opposite end, females of varying estrual states were released. A large proportion of the estrual females sought the ram, solicited copulation, and allowed it to occur; this phenomenon was also related to the age of the ewes in that the older females (i.e. more sexually experienced) allowed more copulations. Failure to recognize the importance of female appetitive behaviors in initiating consummatory responses in rams was originally criticized by Lindsay and Robinson (1961).

“It has generally been assumed that the ram is the aggressor in sexual behavior and that he actively seeks out oestrous ewes which he detects in some manner...From the observations reported here it is apparent that the ewe is a much more aggressive partner than has generally been recognized. (Lindsay and Robinson, 1961, pg. 144).”

Cows in estrus also actively seek the company of males (de Alba and Asdell, 1946) and also mount the male during early estrus (Sambraus, 1971, translated and cited by Blockey, 1976a). These observations would support the hypothesis that formation of the sexually active group and mounting by females is appetitive and serves to change the spatiotemporal relationship between them and their sexual partner(s).

Little attention has been paid to factors that may influence bull sexual attractiveness. The possibility exists that females may show preferences for certain males over others. Blockey (1975) was interested in exploring social dominance factors affecting sexual behavior and fertility in bulls. He cited unpublished data from Osterhoff (1979), who suggested that the dominant bull each year in a group of 3-4, mixed-aged bulls (mingled with an unknown number of cows each year) sired two-thirds of the calves every year for five years, based on results from blood-typing and crossmatching calves back to the bulls to determine parentage. Blockey (1979) went on to report from his dissertation work that overall conception rates were higher when groups of same-age bulls are used in separate female herds, based upon the instability of dominance relationships in younger male animals reared together. It has always been assumed from these and other publications, (Blockey, 1976a,b; Chenoweth, 1981; Lunstra, 1986; Price, 1987) that the females in all of these situations had no influence on limiting

certain males' access to copulation, whether the males were dominant or not. They have always simply assumed that competition among males for the inanimate, passive females determines males' access to them. Perhaps subordinate males elicit fewer approach responses from females or estrual females solicit subordinate males less. In short, the question has never been asked, "Do females find bulls that lose fights or are on a lower social ranking less attractive?" Because of a lack of in-depth questioning, we can only speculate on these statements, with respect to the bovine. In the next section, I review the available literature on sensory systems likely to be involved in providing primary attainment of the appetitive phases of sexual behavior in the bovine, mediated through attractivity.

Stimulus Attractivity through Visual, Olfactory, and Auditory Perception

The suggestion that the sight of mounting activity is the most important visual cue for attracting and arousing bulls has been widely accepted for some time (Hale, 1966; Chenoweth, 1981; Price, 1987; Geary et al., 1991; Geary and Reeves, 1992). In fact, Hale (1966) demonstrated the importance of vision in initiating reproductive behavior in bulls. Eucleating the eyes of one member in each of 6 sets of twin bulls increased latency of first sexual contact. However, all but one of the permanently blinded bulls located females and were successful at copulation. By adapting their motor pattern and investigation methods, after experience with the test paradigm, permanently blinded bulls showed a dramatic increase in the ability to find the teaser animals (Hale, 1966). After considerable investigatory contact and an initial ejaculation, subsequent ejaculations occurred almost immediately in the blind bulls (Hale, 1966). Indeed, all but one blindfolded, normal vision bull ejaculated immediately upon finding the stimulus females, which was much faster, initially, than the permanently blinded bulls. Hale (1966) suggested from these data that visual stimuli facilitate initial responses (i.e. the appetitive phase) but become dispensable after that (i.e. during the consummatory phase). Further studies are necessary to determine whether female/female or male/female mounting also attracts *females* to the vicinity or whether male/male interactions attract females. Perhaps vision regulates the development of the sexually

active group and, hence, provides the initial impetus for females to display their attractivity and begin the cascade of appetitive events leading to copulation.

Geary et al. (1991) placed bulls into rectangular pens divided into unequal thirds and a female in standing estrus was placed randomly in one of the two ends, physically separated from the bull. At the opposite end, a female in diestrus was similarly sequestered. There was no difference in the time bulls spent in close proximity to either female nor were there differences in the expression of flehmen responses (for a description of flehmen response, see section on *The Bases of Stimulus Proceptivity and Receptivity*). Their conclusions were that bulls could not detect putative pheromonal signals in these females and, thus, showed no preference for either a female in estrus versus a female in diestrus (Geary et al., 1991). Twenty-five years before this study was published, Hale (1966) suggested that it would be short-sighted to reach these sorts of conclusions based on observations such as these. Failure to demonstrate a preference between estrual and diestrual females does not mean that the bulls failed to discriminate between estrual and nonestrual odors. A more plausible explanation is that bulls may use other sensory systems to initiate or respond to appetitive behaviors exhibited by attractive females. Perhaps in the study by Geary et al. (1991) the females were not sufficiently attractive to bulls as the females were not allowed to express appetitive behaviors.

The second study by Geary and Reeves (1992) addressed this concern. Geary and Reeves (1992) employed a design similar to that of Geary et al. (1991) but paired estrual females together in sequestered areas to allow female interaction. Bulls spent more time near estrual females that exhibited mounting compared to either a single estrual female or a female in diestrus. When bulls were denied mounting access to females, more flehmen responses were exhibited toward estrual females mounting than either diestrus or estrual females not allowed to mount (Geary and Reeves, 1992). Hale (1966) originally suggested that bulls, either blindfolded or permanently blinded before entering a test pen, failed to detect the presence of a restrained animal based on odor

alone and that vision, audition, or tactile stimulation provided additional, essential cues which eventually allowed most bulls to locate the stimulus animal.

The work of Hale (1966), Geary et al. (1991), and Geary and Reeves (1992) suggested that bulls do not rely on olfaction alone to locate and (or) identify estrual females at a distance. In my view, the latter authors did not completely test the hypothesis that bulls use vision predominantly to identify estrual females; one treatment in the Geary and Reeves (1992) study should have included blindfolded bulls, a technique that has been used successfully to render bulls' vision artificially impaired (Hale, 1966). An additional treatment should have been to render bulls anosmic via olfactory bulbectomy (a technique that was used on rams by Lindsay in 1965) to ablate the olfactory system. In rams, Lindsay (1965) demonstrated that rams' ability to detect estrous females was impaired after ablation of the olfactory system. Anosmic rams approached estrous and nonestrous ewes at random and mated with those that would allow it, whereas intact rams investigated select ewes, and copulated preferentially with those females that had first been detected in estrus, ignoring others in the flock (Lindsay, 1965). Animal welfare concerns and the difficulty of performing such surgeries in bulls may preclude such studies, as suggested by Geary and Reeves (1992).

I have not been able to find any information in the scientific literature that would indicate that bulls have a preference to attempt copulation with the female that mounts or the female standing to be mounted. In early papers describing female sexual behavior, females that were mounting more often than standing were said to be in proestrus (i.e. a short period just before maximal standing estrus) and did not readily allow bulls opportunities for intromission (Rollinson, 1963; Blockey, 1976a). To complicate matters further, Simbraus (1971), Blockey (1976a), and Chenoweth (1983) all acknowledged that even estrual females vary in their willingness to allow copulation. Attempts at intromission by males at times outside of estrus usually are not successful although males may exhibit aborted mounts and other female-directed behaviors readily (personal observation). This contradicts the suggestions of Simbraus (1971) and

Blockey (1975; 1976a,b) who claimed that males will not attempt to mount non-estrous females.

At first glance, these factors suggest a paradox. Bulls are attracted by visual cues associated with a female mounting another who is standing firm. The female mounting is likely to elicit a more dramatic change in the visual field compared to the female standing firm or herd members that are grazing. Thus, the female mounting may be the stimulus that conveys more attractivity to the male, at least initially. However, this female may be less likely to allow mounting and intromission (Sambraus, 1971; Blockey, 1975). As I suggested earlier, bulls may be opportunistic in this sense and maximize the probability of copulation by investigating both females displaying homosexual mounting. Individually testing bulls with unrestrained females of differing receptive states has not been an accepted behavioral paradigm. In fact, there has been little investigation into possible differences in proceptivity and (or) receptivity between females that are standing versus females that are mounting but do not stand to be mounted. Anecdotally, female estrous state is often speculated upon when personnel are attempting to determine standing estrus in bovine females who will be artificially inseminated (Senger, 1999). Under these conditions, it is often suggested that females that are mounting *may* be in estrus (e.g. in proestrus) while those standing firm to mounts *are* in estrus (hence the term, “standing estrus”). Investigation of variable female stimulus conditions and how changes in attractivity affect the expression of bull sexual behavior seems warranted based on these observations.

Very little is known about the effects of auditory perception and processing on the expression of bovine sexual behavior, although female cattle vocalize more during estrus (Price, 1987). Bulls that have been subjected to temporary hearing impairment showed reduced ability to locate receptive females (Blaschke et al., 1984). It should be noted, however, that this procedure failed to completely abolish sexual behavior in these males (Blaschke et al., 1984). In the latter study, the authors suggested that hearing is less important than vision or olfaction in terms of detecting estrus by bulls. However, these tests were conducted in small pens, where visual and olfactory cues

would be exceptionally concentrated. Perhaps in a pasture situation, where distribution of members is extensive, visual, olfactory, and tactile responses are attenuated, and audition could play an exceedingly important role in modulating the initial expression of appetitive behaviors by either the male or the female(s).

At present, there is little, if any, direct evidence that the vocalizations patterns of bovine females vary in accordance with their estrual state, in terms of frequency, amplitude or duration. Fraser and Broom (1990) suggested that female cattle increase vocalizations during estrus to summon and maintain the presence of the bull. Unfortunately, they offer no supporting evidence that would suggest that vocal behavior changes during estrus which fails to support their hypothesis concerning its function. There is certainly no confirming evidence to suggest this occurrence could have direct physiological effects on conspecifics (i.e. auditory biostimulation). In red deer, recorded stag vocalizations consistently advance the date of ovulation in nonsynchronous females (McComb, 1987). It would be interesting to investigate these matters further in cattle.

There has been a tendency to assign hierarchical importance of one sensory modality over another in the animal science literature (Blaschke, et al., 1984; Geary et al., 1991; Geary and Reeves, 1992). Reasons for this are not clear and assigning importance of one sensory system over another could lead to tenuous conclusions (e.g. olfaction is not important in modulating sexual behavior the bull). Olfactory ablation failed to completely abolish sexual behaviors in rams (Lindsay, 1965) and rendering bovine males blind (Hale, 1966) or artificially deaf (Blaschke, et al., 1984) also failed to completely abolish sexual behavior. It is not always clear whether one particular sensory system is effective alone in governing various aspects of sexual behavior. Perhaps it is the interactive context which determines the extent to which sensory systems function in perceiving and processing stimulus attractivity.

Summary of Stimulus Attractivity

The models constructed in Figures 2 and 3 provide a useful approach to characterize and investigate sexual behavior in cattle. This conceptual framework (Pfaus, 1996;

Beach, 1976) recognizes that audition, vocalization, and vision may all be involved in the initiation of the appetitive phase of sexual behavior. Changes in vocalization and homosexual mounting associated with attainment of proximal estrus, in this sense, would increase females' attractiveness value to the male and could directly cause dramatic changes in the spatiotemporal relationship between the mating partners. When females actively pursue or solicit the male or when males investigate the mounting females, contact would then be established and other stimuli (e.g. olfaction and tactile responses) may facilitate further appetitive behaviors which could lead to the consummatory phase. Perhaps determining which sensory modality is most important is not as worthwhile as recognizing that they all have potential roles in facilitating the expression of consummatory behaviors the bovine.

The Bases of Stimulus Proceptivity and Receptivity

One of the most important, eloquent, and germane concepts that Beach (1976) elaborates on with respect to female proceptivity follows verbatim:

“The generalization that each stage of the mating sequence involves reciprocal, bisexual interaction is directly relevant to the nature and causation of female proceptive behavior. When they are in estrus, females not only are most *attractive to the male*, they are most *attracted to him*.” (from Beach (1976), pg. 115, emphasis included).

When I first read this passage, it occurred to me that I had not been completely cognizant of my own misconceptions and bias concerning reproductive behavior between males and females. For now, I will defer my comments on the general bias that exists (and is presently embraced) in the field of animal science to a forthcoming section entitled *A Critique of Traditional Approaches to Measurement of Sexual Behavior in Bulls*. Suffice to say now, that failing to understand the lack of clear distinction between proceptive and receptive female behaviors has led to erroneous conclusions about female sexuality and posits that theirs is an essentially passive repertoire of sexual behavior.

Beach (1976) reminds us that female proceptivity resembles her attractivity in that it consists of appetitive behaviors expressed by the female from stimuli exhibited and perceived from other conspecifics. In turn, appetitive behaviors evoked in this manner would initiate or increase the potential for the male to direct behaviors back toward the female (see Figure 2). Proceptivity is distinct from attractivity in that proceptive behaviors are expressed in order to direct final facilitation of copulation; through coordination and synchronization of postural adjustments to a mount received, genital merger can be maximally realized. Thus, without the expression of female proceptivity, little copulation would occur.

Some caution is warranted here. As we can see from Figure 2, the transition from appetitive to consummatory phases provides useful, albeit abstract, descriptions of general concepts associated with dyadic mating and is supported by extensive research in this area. However, during the actual mating process, appetitive and consummatory behaviors oscillate and the same proceptive response (e.g. lordosis) may be appetitive in one instance and consummatory in the other (hence the reason the Venn diagrams overlap). I reiterate something I wrote earlier; bull mounting behavior has the potential of being both consummatory and appetitive, whereas, it is only appetitive in the female. This, in my view, is demonstrative of the behavioral plasticity that occurs in the bovine mating scenario and, thus, illustrates the value of ethological approaches to studying behavior in terms of providing a more thorough description of these behaviors. The hierarchical, linearized view in Figure 1 (i.e. the view based on precopulatory, copulatory, and postcopulatory behaviors) is becoming less and less useful to us because it inhibits our understanding of the mating process in terms of behavioral plasticity between sexual partners. For example, it would be difficult to define how male precopulatory behaviors (see Figure 1) affect the resumption of female copulatory behaviors since there are no defined female copulatory behaviors. Hence, we are forced to assume that either they do not exist or that they are not important factors in governing overall dyadic mating. The ethological methodology recognizes that female receptivity and proceptivity have the potential to be expressed differently in space and

time and embraces the notion that sexual behavior in the bovine is under the influence of the governing dynamics of sexual partner feedback. Further studies are needed to more thoroughly describe, clarify and quantify the components of these feedback mechanisms.

Proceptive behaviors in the female bovine are extremely subtle and therefore difficult to observe, let alone quantify. An additional factor that hampers understanding bovine sexual behavior relates to the fact that female sexual behavior is largely ignored in the context of dyadic, heterosexual mounting and, thus, there are no complete, highly detailed accounts of proceptive behaviors in the female bovine. Once again, I rely on Beach (1976) and Pfaus (1996) to help with some of these difficulties. They suggest considering female proceptivity in terms of distinct nuances associated with their elicitation mechanisms and their functional significance. Beach (1976) provides detailed descriptions and examples of several categories of proceptive behaviors in nonhuman primates and rodent females but only briefly mentions female bovines in these respects. Beach (1976) elaborates on, *affiliative behavior*, *solicitational behavior*, *alternating approach and withdrawal*, *physical contact responses*, and *mounting by the female*. Below, I attempt to intertwine Beach's (1976) and Pfaus' (1999) theories with the present discussion by detailing each of these categories and suggesting some areas of convergence with respect to the bovine.

Affiliative Behaviors

These are proceptive behaviors conspecifics exhibit to establish and maintain proximity to the stimulus partner but do not directly result in immediate consummatory acts. In primate studies, Peretz et al., (1971) used a scoring method to determine proceptivity in female rhesus monkeys; *Prox* scores were recorded when a female approached and merely sat beside a male. When rhesus females were ovariectomized and treated with estrogen, males within the same cage showed increased *Prox* scores (Phoenix, 1973). As Chenoweth (1981; 1983) and Williamson et al., (1972) have suggested bovine females play the major role in initiating sexual contact. Upon formation of the sexually active group, females engage in many appetitive

behaviors (e.g. mounting, chin resting, etc.); the sexually active group is highly mobile and once contact with males is established, the group remains in close vicinity to them (Williamson et al., 1972). The possibility here is that formation of the sexually active group could be an example of an affiliative response, although caution is necessary here because there have been no detailed discussions of individual proceptive behavior in the female bovine. Frank Beach would likely suggest that affiliative behaviors are unified within the individual partners and not expressed as a group.

Solicitational Behaviors

These are highly species-specific, proceptive behaviors that have also been termed invitational and presentational (Pfaus, 1996). Female solicitation behaviors are characterized by the female assuming the coital posture before any physical contact has been made; in fact, males can be some distance away and females may still display solicitational behaviors (Beach, 1976). The most common soliciting behaviors in female rats include ear wiggling, hopping and darting (McClintock and Adler, 1978; Erskine, 1989). Estrous ewes show a marked tendency for exhibiting strong, male-seeking and solicitational behaviors in that they gather around breeding males and compete for access to the males. Sometimes, they will even wedge themselves between a ram and another female, thus attempting to increase their own attractivity value as a stimulus (Lindsay and Fletcher, 1972).

In the bovine female, there has been little discussion of solicitational displays. Relative to estrual cows, ewes in estrous may display more pronounced proceptive behaviors, as indirectly suggested in the paper by Lindsay and Fletcher (1972). Perhaps repeated “twitching” and elevation of the tail could be considered solicitational behaviors in the bovine; lordosis, however, as a response exhibited mostly after copulation (personal observation), fails to meet the criteria here for solicitational behaviors but certainly could affect latency to further copulations by other bulls. In that sense, as a postconsummatory response, it could solicit sexual attention from other conspecifics. Another possibility is that the lordosis response is simply a reflexive

action that is directly caused by intromission, however, this has not been extensively studied in the bovine.

Approach and Withdrawal

This pattern of female proceptivity is often exhibited by females in a sequence which alternatively adjusts to complementary patterns in the male. Beach (1976) went on to suggest that approach-withdrawal elicits following by the male and is terminated temporally as male appetitive responses ensue. Beach (1975) further stated, if the male does not pursue, a female may attempt another sequence of approach and withdrawal until there is initiation of male appetitive or consummatory response. Clearly, this pattern could stimulate males to pursue and should not be taken as female disinterest in sex or, further, nonreceptivity (Beach, 1976). On the contrary, it is this very interpretation that is often suggested as validation for almost universal adoption of restraining females in bull sexual behavior tests (Blockey, 1976b; Chenoweth, 1981; Lunstra, 1986; Price, 1987). From Chenoweth's (1981) perspective, once a particular bull is attracted to a particular female, and they come into contact, the bull tests her receptivity by chin resting, licking of various areas, and by attempted mounts; any female that is not receptive takes "evasive action" (Chenoweth, 1981; pg. 156). This aspect of bovine sexual behavior, that is, whether females are nonreceptive when they move away from males, or what the threshold is for nonreceptivity after several copulations, deserves further critical investigation. Perhaps female bovines have a lower threshold for several copulations in close temporal succession but, instead, have a higher, overall capacity for copulation with multiple partners. Certainly by restraining females, we could never see this as an important factor governing expression of sexual behavior in this species. Some bulls do show a strong tendency to "repeat breed" unrestrained, estrous cows (de Araujo et al., 2003). In this study, the authors reported that bulls repeat-bred at least one female twice in 92% of tests when bulls were individually paired with 10, estrual females. Godfrey et al., (1989) also reported that most all yearling bulls in their study copulated approximately twice with each estrual female during 6 hours of pasture behavior tests with 15 unrestrained, estrual females.

Mattner and coworkers (1974) observed that bulls would repeatedly mount and copulate with certain estrual females, while ignoring other females who were in standing estrus. Perhaps females that receive repeated copulations exhibit approach and withdrawal responses more readily compared to females that have not yet copulated. Further research is needed to elucidate variation in differences in mating patterns among bulls and how this could influence female sexual behaviors, resumption of subsequent copulations by the male, and, ultimately, overall pregnancy rates of the beef female herd.

Physical Contact Responses

There seems to be widespread instances of female proceptivity manifested through various forms of direct contact behavior before the consummatory phase commences. Investigation of the male's anogenital region, flanks, and the penis are common in several species. In many instances, females contact the penis with various parts of her body included the nose, mouth, tongue (Beach, 1976). Apparently, in some primates, females will grasp the penis with their hands resulting in ensuing consummatory responses (Dixson et al., 1973). Hess (1973) documented cases where female gorillas manipulated the penis with their hands and, in some instances, exhibited fellatio responses.

In the bovine, mutual attractivity occurs and the appetitive phase is initiated between the male and female. Stereotypically, when contact is established a series of other adjunctive behaviors may ensue. At times, the process begins with the male and female attempting to investigate the other's external genitalia. The male and female may also orient themselves in a manner that places their noses in close proximity to conspecific perinea, resulting in the pair rotating in an antiparallel fashion (i.e. circling head to tail). Note that this is not a sexually dimorphic behavior and falls under the category of appetitive behaviors for both the male and the female (see Figure 2). Movie Files 1 and 2 show examples of this behavior in the male and female adult bovine. Both the male and the female are intact, and females are estrogenized and in standing estrus. All media files throughout this electronic dissertation are in *.avi format which can be

readily opened by several media file managers available on the internet (e.g. Windows Medial Player®, QuickTime®, Real Player®, etc.).

Seminal fluid can often be observed leaking from the tip of the bull's protruding, but not fully extended, penis (personal observation). At times, it is during the appetitive phase that the female may urinate in close proximity of the male. When urination occurs in close proximity to the male, almost without fail, the bull will place his snout directly into the stream of urine and exhibits flehmen behavior or flehmen response. In a paper reporting the incidence of flehmen response during different stages of the bovine estrous cycle, a total of 802 flehmen responses were observed. Approximately 46% of flehmen responses by the bull occurred within the peri-estrus period (e.g. 3 days before and one day after estrus) whereas approximately 54% occurred when cows were not in standing estrus (i.e. day 2 through day 18 of the estrous cycles; Hradecky et al., 1983). Total and repeated flehmen responses (i.e. flehmen responses displayed in succession with the same female stimulus) were significantly higher in the peri-estrus period. Significantly fewer flehmen responses occurred during nonestrous periods; however, the bull did not completely stop exhibiting flehmen responses (Hradecky et al., 1983). This led the authors to conclude that either estrual compounds (e.g. sexual pheromones) in the urine are also present during nonestrous states or that the flehmen response is not a response solely expressed during and specific to estrus (Hradecky et al., 1983). As I indicated earlier, Geary et al. (1991) found that the number of flehmen responses by bulls denied physical contact with either estrual or diestrual females were not different. One other possibility is that instead of bulls utilizing olfaction to determine estrual state, the flehmen response may be a behavior manifested after males attempt to self-stimulate themselves. This would be considered a behavioral response that functions to maintain the bull's sexual receptivity following copulation. In terms of approaching and investigation of females, bulls utilize senses other than olfaction, whereas, upon contact, exhibit flehmen as part of contact stimulus provided by the female. The final consummatory phase of copulation would then depend more on

Movie File 1

Movie File 2

Movie Files 1 and 2. Examples of antiparallel circling in an adult bull and estrual female. The male and female have oriented themselves in a manner that places their noses in close proximity to conspecific perineia, resulting in the pair rotating in an antiparallel fashion (i.e. circling head to tail for a short period). Note that this is not a sexually dimorphic behavior and falls under the abstraction of appetitive behaviors for both the male and the female (see Figure 2). Incidentally, these files can be played with a number of different media applications that are presently available on the World Wide Web. Females in these *.avi files can be recognized by large, white identification markings that were painted on their right and left sides, respectively. Bulls were not painted in order to allow easier distinction between males and females.

direct contact stimuli provided by a receptive female with an open and lubricated vagina (Beach, 1976).

Flehmen responses are exhibited independent of urination and are not solely expressed by the male. Females also express flehmen responses, although the frequency of expression and function in the female remain unexplored. In cattle, the female(s) will often groom the male and can often be seen licking the preputial area (personal observation). It is under these dyadic heterosexual circumstances that female flehmen responses can occur in addition to those that may occur upon investigation of conspecific females (Haupt et al., 1989). Movie Files 3 and 4, respectively, show examples of male flehmen response.

The function of the flehmen response is very likely associated with the processing of exteroceptive stimuli through sensory modalities associated with the sense of smell. In the bull, as in many mammalian species, there are two main anatomical and neural networks that process this information (Jacobs et al., 1981). The main and accessory olfactory system consists of a highly vascularized and enervated network of neuroepithelial cells which are located within the nasal cavity. Rapid tongue manipulations over the rostral and medial portions of the palate may facilitate passage of fluids into the incisive ducts and also serve to create a vacuum effect, such that samples of fluids are moved back toward the vomeronasal organ (Jacobs et al., 1981). The vomeronasal organ is believed to play a role in processing chemosensory information through detection of pheromonal compounds.

The flehmen behavior is characterized by elevation of the head, closing of the nostrils, and characteristic curling of the upper lip and tongue manipulation against the soft palate. Movement of the maxilla is also evident (Jacobs et al., 1981) and the male appears to be “grimacing” (Ladewig and Hart, 1981).

During the flehmen response, Jacobs et al. (1981) suggested that elevation of the animal’s head, accompanied by vasoconstriction and vasodilation of the vascular tissue surrounding vomeronasal ducts and the vomeronasal organ itself, may dynamically

Movie File 3

Movie File 4

Movie Files 3 and 4. Examples of flehmen response in the adult bull. The flehmen response is characterized by investigation of perineum, vulvae, flanks, or hind feet culminating in the animal raising its head and curling its nares to nearly ninety degrees.

change afferent and efferent pressure differential to move fluid in and out of the complex, respectively. Proceptive bulls will also press their chins on the backs of females and, if the female is sufficiently receptive, and the pair is properly oriented, the bull will usually mount the female's hindquarters (Blockey, 1976a).

Mounting by the Female

Frank Beach's (1976) final category of female proceptive behavior is extremely relevant in the consideration of sexual behavior in the bovine. However, it has rarely been suggested as such within the context Beach (1976) was describing. This type of female mounting is a widespread phenomenon in many ungulates and an extensive paper provides the observation that most mammalian female mounting that is directed at males culminates in females executing thrusting pelvic movements while on some portion of the males' body. In studies by Sambraus (1971; cited by Blockey, 1976a), cows in estrous seek the company of bulls and at peak estrus mount the bull and other estrual cows as well as attempting to mount those who will not stand. About 60% of their [the estrual females'] mounting activity was directed at bulls (Sambraus, 1971, cited by Blockey, 1976a).

The importance of this may not seem clear at first glance. Nonestrous females rarely mount (Blockey, 1975; 1976a) and when they do, they usually mount another female that is probably in estrus. Based on my own experience, rarely have there been cases of diestrous females riding or attempting to mount males (personal observation). Mounting of males is a female proceptive response during heterosexual mating because it clearly is oriented toward the male and very likely intensifies his sexual arousal (Beach, 1976). If so, according to Figure 2, this would stimulate the bull to mount the proceptive female in return. Beach (1976) further suggests that females mounting males indicates female proceptivity because for many species, like the bovine, the frequency and intensity of mounting behavior are much greater when females are in estrus than in any other time in their cycle.

This latter aspect of Beach's (1976) suggestion has been extensively studied in cattle. On days when no females were in standing estrus (verified by no female mounting

activity) bulls roamed around, merely sniffing vulvae in herds of 13-49 females (Sambraus, 1971; cited by Blockey, 1976a,b). Cows that are not in estrus, but cycling, may have a lower propensity for expressing appetitive behaviors. Indirectly, such studies by Esslemont and Bryant (1976), and Hurnik (1987) suggested that when cows are not in standing estrus there was an obvious and dramatic decrease in overall mounting activity. Williamson et al. (1972), conversely, reported that 90% of females not in estrus still mounted other cows in standing estrus. In a study by Alexander et al. (1984), mounting activity decreased during the luteal phase but with the introduction of novel females in standing estrus, detector cows (i.e. cows not in estrus) were stimulated to mount estrual cows on certain days of either their own or their partner's cycle (i.e. day 15, day of estrus, and day 5 of the 21 day cycle, respectively). It is possible that the proportion of cows exhibiting estrus at any one time could have dramatic effects on the motivation of bulls to investigate and attempt copulations. Further investigation into the degree to which females display proceptive behaviors toward males seems warranted, especially in the context of novel stimulus conditions.

Female Receptivity

The term receptivity is often used to describe the female bovine in standing estrus (Blockey, 1976a; Chenoweth, 1981; Price, 1987). The term has been confused and should be carefully defined in relation to the transition between proceptivity and the consummatory phase. I have tried to explicitly suggest, as did Beach (1976), that female proceptivity is distinct from receptivity in that proceptive behaviors are displayed in response to stimuli from other males, and perhaps even other females, in the case of the bovine. Since our model in Figure 2 has a certain fluidity and recognizes the behavioral plasticity that occurs during mating between a breeding pair, the distinction between proceptivity and receptivity is perhaps most important from the following heuristic perspective (Beach, 1976). Receptive behaviors exhibited by the male and female culminate in the consummatory phase of the mating process. As I have previously alluded to, these behaviors are highly species-specific and sexually differentiated. From the female's perspective, the receptive response entails postural adaptation which

maximizes the opportunity to accept the penis of the male into her vagina; conversely, receptivity in the male would comprise behaviors necessary to ensure proper orientation and placement of the penis in the vagina, followed by characteristic thrusting culminating in ejaculation (i.e. consummatory). This interaction between the male and the female, in a general sense, facilitates insertion of the intromittant organ, plus, as Beach (1976) reminds us, ensures that spatiotemporal proximity is maintained long enough so that intravaginal ejaculation can occur. The possibility, then, is that receptivity in the female bovine is not a passive occurrence because by not displaying receptivity, the probability of a successful copulation is greatly reduced.

Perhaps most of the evidence of bovine receptivity comes from data obtained from the ovariectomized or nonestrous cow. Progesterone-dominated female cattle, as I have previously suggested, usually avoid or even actively discourage a bull's attempt at copulation. Requisite to this, she will not allow penis insertion nor actively cooperate with the male if he succeeds in mounting (Beach, 1976). There are extensive examples where ovariectomized females become receptive after administration of various estrogens. In some instances, females are primed with progesterone, which is then allowed to clear circulation, before administration of estrogen. Davidge et al. (1987) documented the expression of estrous behavior of ovariectomized females given various levels of progesterone and then administered the same dosage of estradiol. They reported that prior exposure to progesterone lowered the frequency of occurrence of homosexual behaviors including chin rests (initiated and received), mounts (initiated and received), and firm stands to a mount compared to controls receiving only the corn-oil carrier for the hormone suspension (Davidge et al., 1987). As progesterone levels prior to estradiol exposure increased (i.e. 100 mg, 300 mg, and 500 mg progesterone•cow⁻¹•day⁻¹, respectively) there was a linear decrease in the incidence of all behaviors quantified. To my knowledge, a similar study investigating heterosexual mounting activities, with the same set of steroidal manipulations using ovariectomized females, has not been carried out and likely warrants further consideration.

As Pfaus (1996) reminds us, female consummatory responses can be somewhat ambiguous and indistinct. In female rats, for example, the only noted, unambiguous consummatory response is lordosis, which, in almost all rodents depends directly on physical contact by the male (Pfaus, 1996), although there are some subspecies exceptions (Beach, 1976). Lordosis in the female bovine is not as pronounced upon direct contact by the male. Nevertheless, based on my own experience with close and extensive observation of many hours of bovine copulation, I suggest that females do make minor, at times obscure adjustments to facilitate intromission by the male. The consummatory phase for the male is unambiguous for almost all mammalian species and involves oriented mounting, intromission, and pelvic thrusting culminating in ejaculation. In the next section, I provide a descriptive analysis of the consummatory phase of mating behavior in the bovine.

The Consummatory Phase in the Bovine

At this phase of the mating continuum, the male and the female have now displayed appetitive behaviors increased reciprocal attractiveness thereby establishing mutual self-interest in copulation. The appetitive behaviors exhibited by both individuals serve to bring them into similar, planar fields resulting in dynamic spatiotemporal convergence. When a bull is sexually aroused, the retractor penis muscle relaxes and allows the penis to extend from its normal sigmoidal position; an anatomical diagram elaborates upon this in Figure 4. Other than the overt signs of female appetitive behaviors, one can only speculate on the arousal state in the female bovine. Pfaus (1996) makes a specific distinction with respect to differentiating between sexual excitement and sexual arousal. Sexual excitement, Pfaus (1996) suggests, is a psychomotor response or a heightened state of locomotion in anticipation of sexual contact. Pfaus (1996) goes on to say that sexual arousal is distinct from this and simply involves an increase in genital blood flow. At this point, it is impossible to differentiate these factors in the female bovine, as they have not been thoroughly investigated.

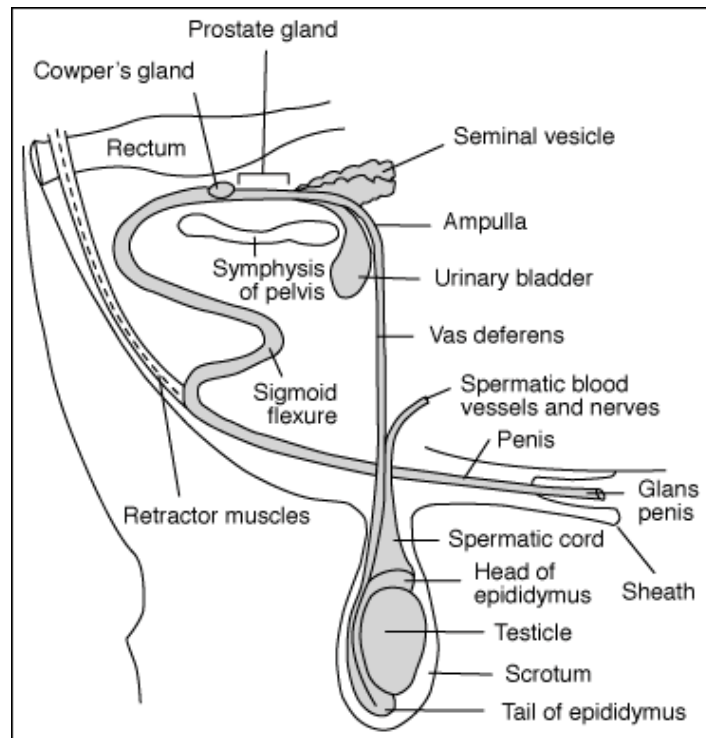


Figure 4. Diagram of the reproductive anatomy of the adult male bovine, detailing the penis retractor muscle and the sigmoid flexure (taken from *Nebraska Guide - G80-536-A*, Issued December, 1980).

Complete copulation (usually referred to as a “service” in the animal science literature) is usually brief, lasting only 1-3 seconds, and is characterized by a properly oriented mount, wherein the male raises his forequarters off the ground, shifting his weight onto his hindquarters, and placing himself on the posterior portion of the female. Simultaneously, the penis is extended, due to the arousal state of the male, and some oscillating motions (i.e. penile seeking) are noted (Sambraus, 1971; Blockey, 1976a). If the female is receptive to copulation she may display some postural adjustments to facilitate intromission (i.e. insertion of the penis into the vaginal orifice). Male intromission is usually accompanied by pelvic thrusting, and at times culminates in a final and deep pelvic thrust, usually indicative of ejaculation (Blockey, 1976a,b; Chenoweth, 1981; Price, 1987). This activity is usually followed by a dismount that can be rather rapid (Chenoweth, 1981; Price, 1987) or, at times, bulls may linger and “slide” off of the female’s hindquarters resulting in a slow dismount (personal observation).

Movie Files 5 and 6 show examples of bulls intromitting with female bovines that are in receptive, standing estrus. In Movie Files 5 and 6, the bull mounts the female, displays intromission, and exhibits a final, deep pelvic thrust followed by a rapid dismount. This series of behavioral events, recall, has been conventionally termed “service”. It is important to note, however, that variation does exist in the expression of these behaviors by the male during the consummatory phase. Bulls may sometimes exhibit intromission but show no overt signs of ejaculation (i.e. no final, deep pelvic thrust), lingering, instead, on the posterior aspect of the female. Movie Files 7 and 8 show examples of copulation wherein the bulls do not display the final deep pelvic thrust and linger for a time on the females’ posterior before dismounting. At times, the male may also display a disoriented mount toward a female which fails to allow the male to achieve intromission. These are referred to as aborted mounts and usually occur anytime the male mounts the head, flank, or rear of the female and fails to achieve intromission, pelvic thrusting or intravaginal ejaculation. Movie Files 9 and 10 shows examples of bulls that have mounted or attempted to mount but have failed to display consummatory behaviors. As one can see, it is difficult to completely rule out the

Movie File 5

Movie File 6

Movie Files 5 and 6. Examples of mounting with intromission and putative ejaculation by adult male bovine. The behaviors are characterized by a mount, penis extension, intromission, thrusting, and a final, pelvic thrust.

Movie File 7

Movie File 8

Movie Files 7 and 8. Examples of variation in copulatory behavior in the adult male bovine. The movie files show examples of bulls displaying mounts, penis extension, and intromission but with no final, deep, pelvic thrust. At this point, it is impossible to determine whether or not ejaculation took place, thus illustrating the ambiguity of the term "service".

Movie File 9

Movie File 10

Movie File 9 and 10. Examples of adult male bovine displaying aborted mounts. Here the male attempts to mount the female but fails to achieve intromission and pelvic thrusting.

possibility that bulls ejaculate inside the vagina without displaying a final, deep, pelvic thrust. Movie File 11 and 12 show examples of bulls who mount, intromit, and appear to have ejaculated without displaying a final, deep, pelvic thrust, evidenced by the withdrawal of the penis followed by what appears to be expulsion of ejaculate.

Postcopulatory Refractoriness and Cessation of Mating in the Bovine

Postcopulatory behavior consists of a refractory period during which the male and female move away from each other and avoid sexual contact for several minutes, although the average time to resumption of sexual activity has not been fully studied in this species. Furthermore, the possibility exists that males and females express a sexually dimorphic refractoriness, a factor that has received little attention in studies with cattle. Perhaps the fact that animals that recurrently mate and then show refractoriness have a reciprocal loss of mutual attractiveness. In this sense, we can use our model once again to suggest that as postconsummatory phases build upon one another, final cessation of copulation is mediated through reduced appetitive behaviors directly influenced by decreases in partner attractiveness. In addition, there may be instances where during periods of sexual satiation, upon interaction with novel incentive stimuli, new bouts of copulation may ensue. Below, I elaborate on a very well known phenomenon associated with this very concept.

The Coolidge Effect – Mythical Beginnings of a Sexual Testing Paradigm

Apparently, the term Coolidge Effect has its original beginnings as a fable about the former President of the United States (Dewsbury, 1981). The fable has also been published in a recent reproductive physiology text (Senger, 1999). I include the fable here for posterity.

“One day President and Mrs. Coolidge were visiting a government farm. Soon after their arrival they were taken off on separate tours. When Mrs. Coolidge passed the chicken pens she paused to ask the man in charge if the rooster copulates more than once each day. “Dozens of times” was the reply. “Please tell that to the President,” Mrs.

Movie File 11

Movie File 12

Movie Files 11 and 12. Examples of adult male bovine displaying an ejaculation without a deep, final pelvic thrust. Here the males mount, intromit, and withdraw a fully extended penis and appear to ejaculate outside the female, without displaying a final, deep pelvic thrust. Thus, this behavior also illustrates the ambiguity of the term “service”.

Coolidge requested. When the President passed the pens and was told about the rooster, he asked, "Same hen every time?" Oh no, Mr. President, a different one each time." The President nodded slowly, then said, "Tell that to Mrs. Coolidge." (Bermant et al., 1968, pp. 76-77; cited by Dewsbury, 1981).

As Dewsbury (1981) points out, an obvious confusion exists here because this fable clearly deals with maintenance of male copulatory activity with simultaneously available females. On the other hand, The Coolidge Effect has become useful in describing reinitiation or resumption of copulation in sexually satiated males who have been with only one stimulus female. Hence, even its beginnings appear to embrace a sexually biased view which assumes female passivity.

Little is known about the mechanisms that regulate frequency of mounting and intromission between dyadic mating interactions. These factors could ultimately determine how bulls distribute their mounting activity over an entire herd of sexually receptive females and could also be involved with determining how much successive copulation receptive females will allow before becoming sexually satiated with a particular male. In many species, the stimulus value of a given partner for a particular conspecific may be temporarily reduced after the pair has copulated several times (Beach, 1976). Behavioral responses associated with the Coolidge effect were first described by Wilson et al. (1963) as a circumstance describing cessation of copulatory activity by the male in dyadic heterosexual mating sequences. Resumption of copulation was readily acquired with the pairing of the male with another receptive female (Wilson et al., 1963). Male rats will cease displaying appetitive behaviors toward a female with which he has displayed several ejaculatory responses. Upon introduction of a novel receptive female, he will promptly resume appetitive behaviors, which may eventually culminate in the consummatory phase (Fisher, 1962). The original female rat is still receptive, however, and stimulus value of other males who have not recently copulated remains high (Fisher (1962). This reinstatement of sexual motivation is much

greater in the case where a novel female is introduced than when the original female is removed and then placed back with the original male (Dewsbury, 1981).

In 1982, a paper by Lisk and Baron, suggested that a phenomenon similar to the Coolidge Effect occurred in female hamsters, and was actually much more robust than the effect seen in male hamsters (Bunnell et al., 1977). There have been few investigations into the possibility that the Coolidge Effect is not a sexually dimorphic phenomenon in the bovine (see Alexander et al., 1984) especially in a dyadic heterosexual mating sense.

The Coolidge Effect has been studied using bulls and results have been summarized (Almquist and Hale, 1956; Hafez et al., 1969; Schein and Hale, 1965). One of two approaches to understanding this phenomenon in cattle has been employed. The first approach used involved allowing bull to copulate to satiety, then exposing them to 1 or 2 novel females in succession (Almquist and Hale, 1956). Almquist and Hale (1956) presented cumulative response curves for three bulls and found that in constant presence of a stimulus female, bulls show a gradual decrease in number of ejaculations per unit time until no sexual behavior was evident. Apparently, loss of sexual response through acute fatigue did not interfere with resumption of copulatory activity since substantial increments were observed in all three bulls upon presentation of a novel female (Almquist and Hale, 1956). In a subsequent study, the same authors observed that the number of ejaculations across 4, 1-hour behavior tests showed little diminution with successive, novel females (Hale and Almquist, 1960). Dewsbury (1981) criticized these studies for lacking appropriate controls and having little to no statistical analyses. Hale and Almquist (1960) also failed to completely describe the stimulus conditions of the teaser animals in terms of sex, gonadal status (i.e. intact or not), receptivity status, or restraint conditions. Hence, while the response to female novelty is appreciable in the bull, additional studies incorporating proper controls and statistical analyses using specified stimulus conditions with either novel or familiar females seem warranted.

As I mentioned earlier, in a study questioning the effects of novel females on female sexual behavior during various stages of the estrous cycle, Alexander et al. (1984) found

that the pairing of novel estrual cows to “heat-detector” cows (i.e. cows not in standing estrus) stimulated mounting activity to a higher degree than when familiar estrual cows were paired with detector cows. Hence, I reiterate the possibility that the Coolidge Effect is not sexually dimorphic in the bovine, a question that has received little attention in the animal science literature but has been readily acknowledged by several researchers using various rodent models (Beach, 1976; Lisk and Baron, 1982).

Other Factors Governing Sexual Behavior in the Bull

Up until now, I have focused heavily on ethological theories associated with sexual behavior. With these considerations, I have tried to develop an understanding of sexual behavior from the perspectives of both the male and female. There is a rather extensive body of research that suggests that there are many other factors that might affect expression of sexual behavior in cattle. As noted above, almost all of the work embraces conventional dualisms about male sexual libido and performance in addition to assuming the male/active, female/passive dichotomy. Examples of factors that affect expression of sexual behavior include hormonal regulation, nutrition, genetic effects, age, social dominance and hierarchies, and male-to-female ratios. It is beyond the scope of this literature review to include an exhaustive account and recapitulation of these topics. Nevertheless, some of these factors are worth discussing in some detail because they have direct bearing on the design of experiments presented in this dissertation. Moreover, an understanding of these factors is useful in interpreting the results of these experiments.

Neuroendocrine Regulation of Sexual Behavior – The Adaptive Behavior Model

Probably the most appropriate explanation for the neuroendocrine regulation of sexual motivation and behavior is the one proposed by Bindra (1974). Agmo (1999) has also provided an extensive review of neuroendocrine factors associated with sexual motivation. Bindra’s (1974) concepts include consideration of two major factors; the *central motive state* and the *central representation of the incentive*. Figure 5 provides a schematic view of Bindra’s concepts. The central motive state is a “hypothetical set of

neural processes that promotes goal-directed actions in relation to particular classes of incentive stimuli," (Bindra, 1974; pg. 201). The central representation of incentive stimuli, according to Bindra (1974), is achieved through a second set of hypothetical neurons that establish the central representation of the stimuli. Hence, in this model, there is a mutually exciting relationship between the partner and the incentive stimulus perceived directly by sensory systems. Perceived stimuli are then processed via specific neuronal pathways which serve to provide central representation of incentive stimuli (i.e. central representation), and interact to affect the motivational state of the animal in space and time (i.e. central motive state), resulting in either approach to or withdrawal from the incentive stimuli.

Through Bindra's (1974) concepts we can now see the intricacies of the models proposed by Beach (1976) and Pfaus (1996) unfolding to reveal the underlying neuroendocrine and endocrine bases for sexual motivation. The central motive state enhances the sensory system's responsiveness to sexual stimuli. Upon perceiving sexual stimuli, the sensory system excites the central motive state. In this manner the reciprocal nature of this relationship is best described in terms of a reciprocal positive feedback (Agmo, 1999). Bindra (1974) proposes that at a threshold level of central motivation and viscerosomatic reactions are taking place which prepare the partners for sexual contact. In the terms of our models (Figure 2 and 3) these may be concerned with, almost exclusively, appetitive behaviors. In these terms, appropriate appetitive stimuli between the sexual partners, the central motive state may activate specific motor patterns that bring the two sexual partners together. During the approach phase other additional stimuli may be encountered (Agmo, 1999). These additional stimuli (e.g. olfactory processing by the bull through flehmen) would then enhance the central motive state further, leading to physical contact (e.g. mounting). At this point, if approach has been made and contact has been proximally established, the partners may proceed with the consummatory phase. Agmo (1999) goes on to suggest that the

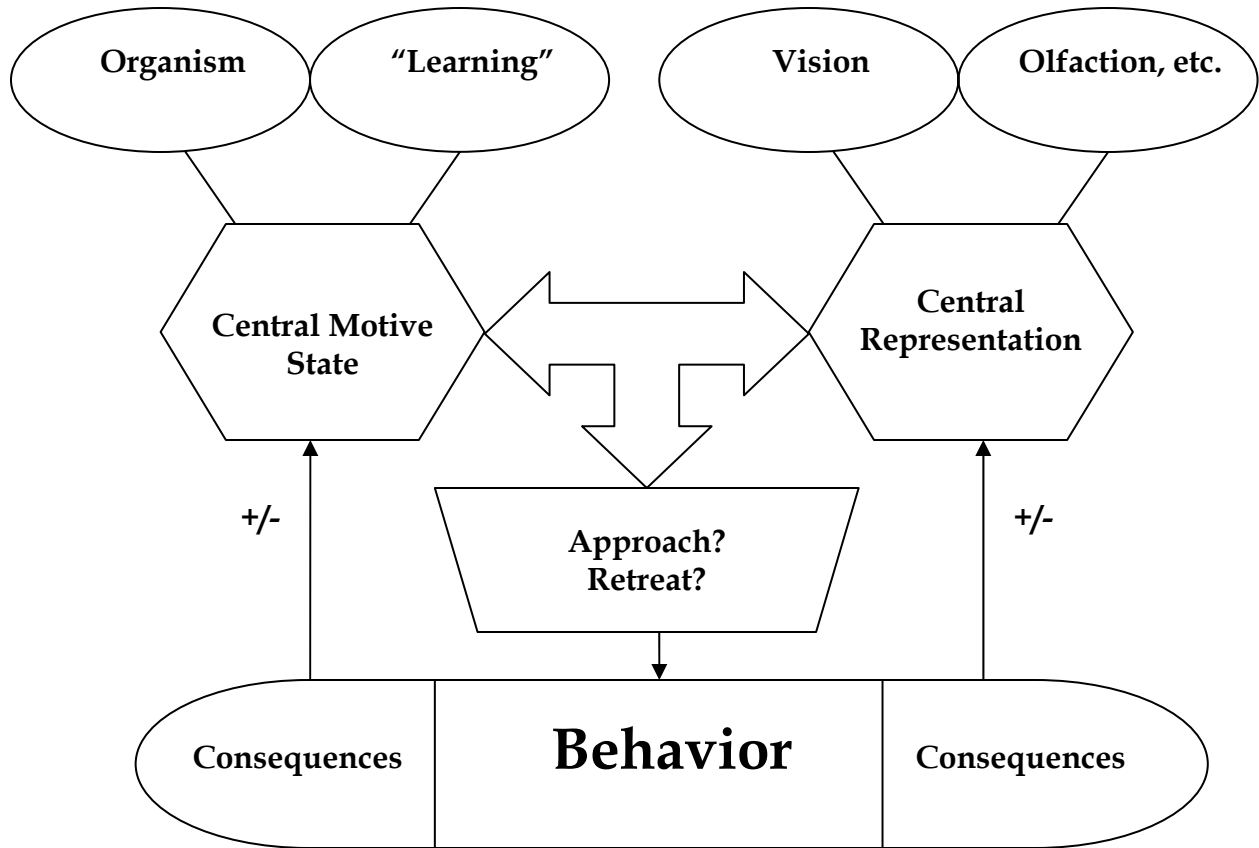


Figure 5. The *Adaptive Behavior Model* proposed by Bindra (1974). Bindra's (1974) concepts consider two major factors; the *central motive state* and the *central representation of the incentive*. In this view, the central motive state is a "hypothetical set of neural processes that promotes goal-directed actions in relation to particular classes of incentive stimuli," (Bindra, 1974; pg. 201). The central representation of incentive stimuli, according to Bindra (1974), is achieved through a second set of hypothetical neurons that establish the central representation of the stimuli. Hence, in this model, there is a mutually exciting relationship between the partner and the incentive stimulus perceived directly by sensory systems. Perceived stimuli are then processed via specific neuronal pathways which serve to provide representation of incentive stimuli (i.e. central representation), and interact to affect the motivational state of the animal in space and time (i.e. central motive state), resulting in either approach to or withdrawal from the incentive stimuli. The consequences of the behavior may impart positive or negative re-enforcement either through the central motive state, central representation of stimuli, or, perhaps, both.

execution of sexual reflexes is activated by tactile stimulation of perineum. If tactile stimulation is precluded, the behavioral sequence is aborted prior to the consummatory phase. In Bindra's (1974) model, if sexual reflexes (i.e. intromission, ejaculation, etc.) are activated and completed, ejaculation may feedback to the central motive states of both partners where a short, postejaculatory inhibitory system is activated, resulting in, at times, a transient decrease in partner attractiveness (Beach, 1976).

Another important concept in Bindra's (1974) theory is associated with learning, experience, and consequences. Positive effects and the associated aspects of reinforcement influence learning of the association between the partner and the incentive stimuli. Under this view, stimuli perceived directly from appetitive behaviors expressed by the partner or behaviors expressed during execution of copulation itself, acquire more incentive properties (Agmo, 1999). The resumption of sexual activity as the partners gain more sexual experience is directly related to the intensity of the positive incentive properties of the incentive stimuli and the consequences of consummation (Bindra, 1974). One can also see how negative reinforcement could result from association between the partner, negative incentive stimulus properties, and consequences of consummation.

It is important to realize that volumes of work have been conducted and published determining the neuroendocrine and endocrine factors corroborating Bindra's (1974) concepts. It is well beyond the scope of this dissertation to provide exhaustive explanation of the available literature concerning humoral factors influencing the central motive state and central representation of incentive stimuli using rodent models. I will simply emphasize the general concept; the central motive state is most likely dependent on gonadal steroids and central neurotransmission. There is overwhelming evidence that androgens and estrogens in the male and estrogens (and in some instances progestins) in the female are necessary for sexual motivation (Agmo, 1999). In addition, not only is motivation affected by gonadal steroids and monoamine neurotransmitters but also normal display of certain consummatory behaviors (e.g.

intromission, ejaculation, lordosis in the rodent, etc.) may also be influenced directly by these humoral factors (Bindra, 1974; Beach, 1976; Agmo, 1999).

Recently, De Vries and Boyle (1998), Hull et al. (1999), Imwalle et al. (2002) and Scordalakes et al. (2002) have all described neurotransmitter systems that potentially mediate the effects of gonadal steroids on sexual and other socially mediated behaviors. The size and number of neuronal cell bodies, distribution and concentration of certain neurotransmitters (e.g. dopamine, adrenaline, nitric oxide, etc.) in areas such as the medial preoptic area, ventromedial hypothalamus, nigrostriatal and mesolimbic areas are all potentially important anatomical areas that influence sexual behavior. To my knowledge, research designed to investigate these topics in livestock have not been conducted. Moreover, only one investigation (Imwalle and Schillo, 2002) has attempted to apply Bindra's (1974) concepts to investigate reproductive behavior in the bovine.

Consideration of Male to Female Ratios

Bull-to-female ratios in natural breeding herds are important management considerations especially in the Western United States. For example, in one study single- and multiple-bull breeding systems were compared using Hereford bulls at male to female ratios of 1:25, 1:44 and 1:60. Semen characteristics and copulation proficiency of individual bulls were more important than either male to female ratios or using a single vs. multiple-bull breeding system in determining pregnancy rates (Rupp et al., 1977). In a Colorado study, yearling Hereford bulls which had been pre-assessed for breeding soundness (e.g. evaluation of sperm gross morphology, structural soundness of the male, etc.) and found acceptable for breeding, were used in pasture breeding scenarios using male to female ratios of 1:20 and 2:40 with estrus-synchronized heifers (Farin et al., 1982). Bull mating proficiency and pregnancy rates were not affected by male to female ratios. Using a variety of male to female ratios (1:7 to 1:51), with estrus synchronized females, Pexton et al. (1990) found that male to female ratios were not a limiting factor to herd fertility, even at the lowest ratio in single-bull mating.

In contrast, another study suggested that lower herd fertility may occur when male to female ratios exceed approximately 1:50 (Healy et al., 1993). In this study, estrus synchronization failed to provide any advantage in either pregnancy rates or conception day in a 28-day breeding season with cycling, yearling beef heifers and 2-5 year old bulls of 1:50 (Healy et al., 1993). Although estrus synchronization has proven to be a valuable tool for enhancing reproductive efficiency by shortening the breeding and, consequently, the calving seasons, this practice also increases the breeding pressure or mating load that bulls are exposed to. Healy et al. (1993) suggested, some bulls may not be able to effectively impregnate all females when a large number of them are in estrus and receptive simultaneously. There were no attempts in the Healy et al. (1993) study to determine individual differences in sexual behavior of bulls nor were bulls evaluated from a dominance hierarchy perspective. More research is needed to investigate the optimal interactions between maintenance of bull sexual behavior during the breeding season and optimal male to female ratios, especially when estrus synchronization of females is employed.

Copulation Frequency Scores in Restrained Female Tests and Fertility in the Male Bovine

The ability of bulls to detect estrual females and the behavioral pattern of copulation and ejaculation are two of the most important contributing behavioral factors that can influence overall herd fertility. One hypothesis associated with distribution of copulation and ejaculation is that bulls distribute themselves equally among receptive females, copulating with each 1 or 2 times (Blockey, 1976a,b). Another hypothesis is that sexually mature bulls “repeat breed” many estrual females (de Araujo et al., 2003) before becoming sexually satiated; bulls would then move to different estrual females and repeatedly copulate with other estrual females.

Blockey (1976a,b) suggested that if bulls distribute their copulations equally among receptive females, their sexual efficiency during mating at pasture could best be measured by their individual “serving capacity”. This was a measure of the number of “services” a bull achieves in 7.5 hours of pasture mating with unrestrained,

estrogenized heifers. Blockey (1976 a,b,c) then devised a shorter test for predicting “serving capacity” by restraining females in “service crates”, sexually stimulating bulls by allowing them to visually observe other bulls copulating with the restrained females, and then counting the number of “services” each bull achieves in 40 minutes. These tests were referred to as “yard tests” and the resulting measurements were also termed “serving capacity” (Blockey, 1976b; 1981a,b,c). I will differentiate between the measurements obtained therein as either “pasture serving capacity” or “yard serving capacity”.

Blockey (1981a,b) found high correlations ($r = 0.82$ to 0.91) between “yard serving capacity” and the number of “services” by each bull in the first 3 weeks of a pasture mating period. In of his studies, first-cycle pregnancy rates were higher in heifers mated with bulls displaying higher “yard serving capacities” than in females mated with bulls exhibiting lower ones (Blockey, 1978a). Differences in pregnancy rates were also demonstrated between Hereford bulls with high, medium and low “yard serving capacities” (Blockey, 1989). Other breeds of bulls having acceptable semen characteristics and higher copulation frequency during restrained female tests were also found to influence pregnancy rates (Makarechian and Farid, 1985; Lunstra, 1986; Smith et al., 1981).

In addition, studies have indicated either assessment of bull copulation frequency with restrained females provided greater prediction of overall bull fertility than did semen assessment alone (Smith et al., 1981), or that it augmented traditional breeding soundness evaluation (Spitzer et al., 1988). Using multiple-bull mating and progeny identification by blood typing (which was 40-85% accurate), the number of copulations performed in “serving capacity” tests with restrained females was positively correlated with fertility up to a level of approximately four copulations (Coulter and Kozub, 1989). Interestingly, above this level of “yard serving capacity” fertility declined in a curvilinear manner (Coulter and Kozub, 1989). These results suggest that bulls displaying few “services” during “serving capacity” tests likely inseminate few females during pasture mating. However, bulls that display very high numbers of “services”

during yard testing do not sire as many calves at pasture compared to bulls displaying moderate numbers of “services”. This could be due to differences in behavioral patterns expressed by some bulls that repeatedly breed females for an relatively longer period of time, which could result in some estrual females not being bred before termination of their estrual state or inseminating some females with too few spermatozoa (Coulter and Kozub, 1989).

Other investigators have shown poor relationships between bull copulation frequency during yard tests (with restrained females) and either overall herd fertility or bull copulation frequency at pasture (Boyd et al., 1989; Christensen et al., 1982; Chrichton et al., 1987; Makarechian et al., 1987; Farin et al., 1989). In the Farin et al. (1989) study, breeding soundness exams were conducted on 92 beef bulls that were categorized as either satisfactory or questionable; unsatisfactory bulls were not used in experiments. Prior to single-bull mating with groups of estrus synchronized heifers “serving capacity” tests with restrained females were also conducted (Farin et al., 1989). Using a subjective scoring index developed by Chenoweth et al. (1979), bulls were ranked with respect to individual “yard serving capacity”. (Farin et al., 1989). Overall pregnancy rates were 9.1% higher for bulls deemed satisfactory by the breeding soundness exam compared with bulls that were questionable (Farin et al., 1989). Pregnancy rates did not differ between bulls of high and medium “serving capacity” index scores; however, bulls scoring higher on the index scale copulated more often and with more females than did medium scoring bulls (Farin et al., 1989). Lower pregnancy rates in females mating to bulls of high “serving capacity” occurred because a lower percentage of females in the group mated with these bulls became pregnant compared to the group with bulls of lower “serving capacity” index scores (Farin et al., 1989). In a section below, I give a clearer account of the assumptions embraced by investigators using “serving capacity” tests. Embracing certain assumptions regarding female sexual passivity might affect our views concerning overall beef herd fertility.

Social Effects and Dominance Hierarchies Among Bulls

Social ranking within groups of bulls can influence their sexual behavior (Rupp et al., 1977; Blockey, 1975; 1979; Chenoweth, 1981; Farid et al., 1983). Apparently, dominance values are more stable and expressed linearly in bulls older than approximately 3 years of age compared to younger bulls. Dominance among breeding bulls may be related to body weight and age (Bouissou, 1975) although dominance may be more related to seniority than to either age or body weight (Blockey, 1979). Blockey (1979) further suggested that the effect of agonistic social interactions among bulls on herd fertility may be greater when there are fewer total females in the breeding group.

Dominance effects among bulls can also influence results obtained in pen tests for bull sex drive (Imwalle, 2000; Imwalle and Schillo, 2002) and may even negatively impact herd fertility (Blockey, 1975). This effect could be mediated through overall failure to copulate with estrual females or by bulls with lower fertility preventing subordinate, fertile bulls from copulating. Blockey (1979) also suggested that these effects have the greatest probability of occurring when breeding males are combined in a mixed aged fashion in the breeding pasture.

Paradoxically, some researchers report that testing more than one bull, or having bulls observe other bulls mounting, may be beneficial to bull sexual behavior. This was observed in studies where greater sexual activity occurred when young, inexperienced bulls were tested in groups (Price, 1987; Godfrey and Lunstra, 1989). It has been readily assumed that the combination of bull prestimulation (e.g. visually observing other bulls copulating with restrained females) and competition can positively influence results of commonly used “serving capacity” tests. Studies designed to test the hypothesis that dominance among males influences female sexual receptivity or preference seem warranted based on these observations.

Summary of These Additional Factors Affecting Herd Fertility

Almost all of the research I have mentioned in the previous section has sought to meet the utilitarian goals of the researchers, namely, to quickly and efficiently identify

bulls that have a greater potential to impregnate females during the breeding season. Pregnancy rates under management conditions are extremely variable. Smith et al. (1981) found that placing individual bulls among several herds of approximately the same number of cycling females, resulted in divergent pregnancy rates (0-85%). Lunstra (1986), in a similar study, showed that among 12 bulls with similar semen characteristics, body weights, and other phenotypic traits, pregnancy rates when exposed to similar numbers of cycling females, again, were highly disparate (0-95%). Some of this variation in pregnancy rates, they suggested, could be influenced by the expression and pattern of bull sexual behavior in conjunction with copulation frequency.

By reviewing 10,940 breeding soundness exam records, Carroll et al. (1963) found that 79.2%, 11.2% and 7.2% of bulls were satisfactory, questionable, or unsatisfactory, respectively. Another similar study by Spitzer et al. (1988) reported that 80%, 7.3%, and 12.7% of bulls fell into those categories, respectively. In order to maintain, much less enhance, reproductive efficiency producers should assess the reproductive capabilities of breeding bulls. Although there is a long standing, highly repeatable, acceptable means to determine overall gross sperm morphology, locomotion ability, and other traits evaluated in the breeding soundness examination, they are not commonly used by producers. A study published by the National Animal Health Monitoring System (NAHMS, 1997), which covered approximately 85% of all cattle in the United States, reported that less than 40% of beef producers utilize the breeding soundness exam. Three primary reasons were cited for not using the exam in commercial operations; 1) time and labor, 2) interpretation of results, and 3) additional monetary cost. It is very clear that while the breeding soundness exam is effective in distinguishing among bulls' reproductive capabilities in terms of semen qualities and overall structural soundness, recommendations do not currently reflect the need to incorporate tests of copulatory proficiency.

Blockey (1981a,b) advocated the use of Breeding Soundness Exams in conjunction with testing potential breeding bulls' sexual behavior using his modified "serving

capacity” test. Based on the interrelationships among seminal quality, expression of sexual behavior and presently accepted male to female ratios and their impacts on reproductive efficiency of beef herds, I agree that there is a need to further investigate how these factors interact to affect profitability in beef herds. However, the methods advocated by Blockey (1981a,b,c) are not an appropriate means to accomplish this goal.

In the next section, I describe the historical development of methods to quantitatively assess bulls’ copulatory efficiency and follow this discussion with a description of the so-called “Serving Capacity Test” developed by Blockey in the mid-1970s. Afterwards, I offer a critical analysis of these presently accepted methods of testing male copulation frequency using restrained females.

Development of Quantitative Tests for Consummatory Behaviors in the Male Bovine

Copulation frequency in bulls has been assessed in a number of ways. The simplest method is simply to observe a bull in a confined area with one or several restrained females either in estrus or not (Blockey, 1975; Chenoweth, 1983; Price, 1987).

Quantitative assessments include reaction time to first behavior (mount, intromission, ejaculation, etc.), and “serving capacity” (the number of intromissions accompanied by a final, deep, pelvic thrust; also known as a complete copulation under stipulated conditions), mating ability (ratio of mounts to copulations), and exhaustion tests (copulation rate over time until sexual exhaustion) (Chenoweth, 1981).

Apparently, the development of a system for quantifying ejaculation rate arose during the 1950s in association with development artificial insemination methodology. The primary impetus for development of artificial insemination was to reduce animal related injuries on dairy farms; dairy bulls are aggressive and dangerous to handle, and caused many injuries and even deaths of personnel (Casey et al., 1997). From this concern came the establishment of artificial insemination centers that collected and stored semen periodically collected from bulls that were trained to mount either “dummy” objects or teaser animals to facilitate collection using an artificial vagina.

Decreased copulation frequency following repeated semen collection led to an interest in developing methods to identify bulls that could maintain their sexual activity for prolonged periods. This would allow a more uniform collection of semen for all bulls at these artificial insemination centers and eliminate bulls that were poor producers. Using various techniques meant to increase sexual stimulation (Chenoweth, 1983) bulls that did not elicit sexual responses could then be culled. Techniques associated with sexual preparation (e.g. false mounting, etc.), as Chenoweth (1982) suggests, was designed to maximize the concentration of spermatozoa in a particular ejaculate from those bulls that were not culled based on sexual response. Hence, by utilizing both stimulatory and preparatory techniques, high quality and less variable ejaculates could be harvested and stored from bulls that were repeatedly collected over long periods of time. Beef bulls, on the other hand, did not show the same maintenance of copulatory activity and over repeated ejaculates required frequent changes of incentive stimuli to reach similar levels of semen collection (Almquist, 1973).

Early researchers interested in optimizing semen harvests attempted to provide an easier method of identifying bulls that could copulate frequently. To accomplish this goal, "libido index" methodology was used to assess both libido and mating ability in bulls at artificial insemination centers (Hultnas et al., 1959). For example, a bull that was scored with a zero showed no interest in a teaser cow even though the bull was led up to and invited to mount; bulls scoring a 6 on the libido index showed uncontrolled extremely eager mounting, exhibiting intensive penile seeking events (Hultnas et al., 1959). Subsequently this method was modified to include other factors of behavior and termed "libido score", which was used for assessing range-type beef bulls (Osbourne et al., 1971). This procedure (i.e. the "libido score" test), used estrogenized, unrestrained females to assess "libido score" in bulls used for pasture breeding (Osborne et al., 1971). This was later expanded to a 0-10 scoring system which described degrees of sexual interest within a 10-minute test (Chenoweth et al., 1979). For example, a score of zero denoted no sexual interest in restrained teaser females whereas a score of 10 indicated that a bull displayed 2 "services" followed by sexual interest, including mounts,

mounting attempts or further “services” (Chenoweth et al., 1979). Other tests were based on the number of “services” achieved (Blockey, 1976b , 1981a,b,c) under stipulated conditions either in a yard or at pasture (see section below on *Development of the “Serving Capacity” Test*).

Enumerating each and every test ever conducted becomes so convoluted and confusing that it would detract from our present focus. Suffice it to say, there have been many composite procedures employing elements of all of the first sexual behavior tests which have been used to evaluate young *Bos taurus* and *Bos indicus* bulls. These procedures employ various elements such as visual stimuli, induced competition between bulls, and severely restrained and sedated females, all with the purpose of identifying the bulls that will copulate the most and the fastest under these conditions. Failure to critically evaluate these methods has led to almost total acceptance of them and in doing so, precludes development of a comprehensive account of sexual behavior in cattle. In the next section, I describe, in some detail, the development of the original test for bulls’ “serving capacity”. In the section following description of these tests, I offer some points of criticism of this methodology.

Development of the “Serving Capacity” Test

In Australia, during the mid 1970s, M.A. de B. Blockey, a veterinarian, was pursuing doctoral work aimed at increasing profitability of beef production. Blockey (1975) theorized that by improving our selection criteria for herd bulls, higher reproductive efficiency could be realized and, thus, reduce production costs. Since beef producers have little to no idea what a particular bull’s copulatory efficiency would be, Blockey (1975) proposed that a worthwhile endeavor would be to develop a means to quantify such behavior. After publishing his review on sexual behavior of beef bulls at pasture (1976a), Blockey concluded that most producers determine the effectiveness of their breeding bulls by simply tabulating the number of successful pregnancies and figuring a calving percentage for the herd. Blockey’s (1976a) criticism of this approach to determine a bull’s quality as a herd sire was that pregnancy rates don’t reflect how many times a particular bull mounts estrual females, nor does it give information about

the success ratio of bulls (i.e. the cumulative percentage of how many females are detected in estrous, inseminated, and give birth to a live calf). With these practical goals in mind, he devised a "serving capacity" test.

Blockey's (1975) first objective was to describe the social aspects of cohort groups of bulls, determine their social ranking, and investigate whether these rankings had influence on their sexual access to females (Blockey, 1975). Secondly, Blockey (1975) wanted to observe mating behavior of bulls at pasture with a herd of receptive females and document how many times each bull would copulate with the ovariectomized, estrogenized females. His third objective was to develop a rapid, practical yard test that would accurately predict bulls' sexual behavior at pasture (Blockey, 1975). Other objectives were to determine the importance of sexual testing with respect to veterinarian examination, investigate the influence of breed and muscle or joint abnormalities on sexual behavior and, finally, study the hormonal control of "serving capacity" (Blockey, 1975). My discussion will be confined to his second and third objectives.

To meet his second objective, Blockey (1975) utilized 53 ovariectomized heifers given a single injection of estradiol benzoate to induce estrus. Bulls of varying age and sexual experience were placed with the females in 2 hectare pastures or paddocks (Blockey, 1975). As I stated before, the term "service" was originally defined by Sambraus (1971) and translated by Blockey (1975) as any motor pattern that results in the male lifting his forequarters off the ground, clasping the female's pelvis, and bringing the tip of the erect and protruding penis near the vaginal orifice. After displaying a series of oscillating motions, the penis penetrates the vaginal orifice, resulting in a lengthening of the penis (due to relaxation of the penis retractor muscle and straightening of the sigmoid flexure) followed by one or more intromissions leading to ejaculation (Blockey, 1975). During ejaculation, the male will often display a final, deep pelvic thrust during which the bull lifts his hindquarters completely off the ground (adapted from Blockey, 1975). Observers recorded the bull and heifer identification numbers anytime there was an event where the bulls exhibited this behavior. After 7.5 hours each bull was ranked

according to his “serving capacity” (Blockey, 1975). There were four herds of bulls used (n=18, 30, 18, and 9, respectively). Bulls in one herd were reused in subsequent herds for unspecified reasons.

The same 53 females were repeatedly used in all 4 pasture tests, although not all females were used each time. The interval between pasture test 1 and 2 was 7 days whereas the interval between tests 2 and both 3 and 4 (conducted on the same day) was 6 days. Based on simple correlations, Blockey (1976b,c) concluded that the total number of females “serviced” by a particular bull was highly and positively correlated with the total number of “services” each bull exhibited during the 7.5 hours of pasture mating (i.e. bulls distribute their “services” equally among receptive females).

To meet his third objective, which was to devise a simple, quick, efficient yard test to predict bulls’ behavior at pasture, Blockey conducted a test in a small, enclosed yard with unrestrained females. Blockey (1975) criticized this approach because he could not find the proper relationship he was looking for among the bulls. In other words, he could not differentiate between low, medium, and high “serving capacity” bulls, which he had already determined during the pasture mating trials. Additionally, only 3 of 12 bulls responded to the unrestrained, ovariectomized, estrogenized females (Blockey, 1975; 1976b). Blockey (1975; 1976b) sought to reduce the variation of responses he had seen during pasture mating. For example, some females, after copulating several times, would not allow further copulations from other bulls and some bulls were prevented from copulating by more dominant bulls (Blockey, 1976a,b). Bulls spent a considerable amount of time courting receptive females (Blockey, 1976a,b). Blockey (1976b) suggested that utilizing restrained, estrual females would reduce the time needed to test bulls because it would eliminate the need for bulls to court receptive females (Blockey, 1976b). Effectively, Blockey (1975; 1976b) could test the same number of bulls in a shorter amount of time (i.e. 3 hours).

Finally, Blockey (1976b) could make the behavior testing of bulls more practical by testing more bulls than restrained females during each test. Hence, by restraining females in “service crates” or with ropes and posts at each shoulder and allowing more

males than restrained females to copulate at will for 3 hours, Blockey (1976b) eliminated female and male appetitive behaviors, thereby shortening the amount of time needed to test and rank bulls according to their “serving capacity”. It is important to realize that by adopting this methodology, Blockey (1976b) also eliminated females’ role in the mating process. Blockey (1975) devised this “yard serving capacity” test with the objective of obtaining measurements that were highly correlated with the “pasture serving capacity test”. Since a bull’s “serving capacity” was the number of “services” it achieved during pasture mating, he suggested the appropriate measurement would be numbers of “services” displayed by the bulls during these shortened tests (Blockey, 1976b).

After removing various males from the correlation analyses, for either lameness or short penile protrusion, Blockey (1976b) reported high correlations ($r = 0.91, 0.92,$ and 0.92) between bulls’ pasture “serving capacity” and their 1, 2, and 3 hour cumulative “service” score in the yard “serving capacity” test. We can see that this view is diametrically opposed the ethologists’ view in that Blockey (1975; 1976a,b,c) was only interested in the frequency of male consummatory behaviors and how fast and efficient bulls could distribute them in a short period of time, thus allowing a rapid method for determining which bulls could copulate and a method for ranking them according to this performance. Females are not considered important participants in sexual behavior and are assumed to have no role in controlling sexual behavior of the bull in these “serving capacity” tests.

Critique of Conventional Approaches of Quantifying Bull Sexual Behavior

In both his dissertation and the publications resulting from it, Blockey (1975; 1976a,b; 1978; 1979a,b; 1981a,b,c) correctly asserts that hypotheses about the relationship between bull sexual behavior and overall beef herd fertility, in addition to factors controlling sexual behavior, are scarce. In attempting to rectify these deficits, he sought to develop a quick, efficient, and repeatable method for determining and predicting bull copulatory proficiency under pasture conditions. In short, he wanted to develop a test that producers could use on their own farms or ranches that would eliminate some of

the “guess-work” associated with a particular bull’s potential to increase herd fertility. He supported these objectives with data obtained primarily from his own dissertation work and obscure publications requiring translation to English (Sambraus, 1971; Wohanka, 1968).

The purpose of this section is to critically evaluate the reasoning that Blockey (1975) used to develop the “serving capacity” test to which many other researchers over several decades have assumed to be correct (Chenoweth et al., 1979; Christensen et al., 1982; Lunstra, 1986; Coulter and Kozub, 1989; Landeata-Hernandez et al., 2001; Bertram et al., 2002). Through such a critique, I hope to illuminate important popular misconceptions about sexual behavior of cattle.

Critique of Conventional Approaches Using Ethological Perspectives

With respect to research concerning sexual behavior of cattle, several things are presently needed and in my opinion ethological perspectives appear useful in meeting these needs. For example, there is a need for hypotheses that are specific and not global. Any hypotheses associated with the expression of sexual behavior of bulls must take into account the notion that male and female bovine copulate in an oscillating, dyadic heterosexual manner, involving appetitive and consummatory phases of sexual behavior. Therefore, in order for hypotheses concerning the control of sexual behavior in cattle to be meaningful, they should specify which phases of copulation are being observed, or manipulated, and how this manipulation affects the expression of sexual behavior in the dyad. Female bovines are not simply “inverted, U-shaped objects (Chenoweth, 1981; Price, 1987) nor are they homogenous and identical. Yet by restraining and sedating them, investigators embrace the notion that male and female appetitive behaviors are negligible and the most important aspect for study is male consummatory behavior and its frequency and rate of expression. If this is the case, the hypotheses should state this specifically.

Secondly, hypotheses should be correctly supported by direct observations and data. For example, recognizing that males and females are interacting during the appetitive and consummatory phases requires that we recognize they are both equally active in

the mating process. If females are reducible to inverted, U-shaped objects, then the appropriate apparatus to use during bull sexual behavior testing should be an inverted, U-shaped object (e.g. mounting dummies, etc.) to quantify and rank bulls based on their sexual behavior. In addition, under the restrained female methodology, there should be no statistical difference in the expression of bull sexual behavior between conditions using live females versus mounting dummies. This hypothesis is readily assumed yet has not been fully tested. Furthermore, if we deem a particular behavior as a complete copulation, we must be able to verify that ejaculations are not taking place outside of this specific behavior. Describing bull sexual behavior utilizing the term “service” fails in this regard. Utilizing terms such as mounts with or without intromission and mounts with intromission followed by a deep, pelvic thrust seem to be better suited for describing and quantifying bull consummatory behavior.

Thirdly, hypotheses and results should be expressed in such a way to integrate complex data rather than reduce them to their simplest form by ignoring or overlooking important distinctions. For example, dominance among bulls seems to be an important factor in determining which bulls copulate with receptive females (Blockey, 1975), yet, by testing groups of bulls together with restrained females, dominance factors are ignored (Blockey, 1976b; Price and Wallach, 1991a,b,c). How would we know the extent to which the expression of bull sexual behavior is influenced by dominance *per se* and not developmental factors such as failure to display sexual behavior during critical periods of development due to dominance among herdmates?

Additionally, the assumption that restraining females in “service crates” or “service stanchions” removes their ability to inhibit the expression of sexual behavior by the bull, thereby causing the male to express his “inherent sexual desire”, has been suggested as a justification for conventional methods used by many authors (Blockey, 1976b; Chenoweth et al., 1981; Price, 1987). However, inherent sexual desire is an abstraction and is only manifested as a function of experience and coordination of this mating experience within the context of dyadic copulation; this has not been explicitly acknowledged in any paper concerning the expression of sexual behavior in the bull.

A highly detailed description of sexual behavior manifested during dyadic heterosexual mating in the male and female bovine would add to our present discourse concerning reproductive fertility of beef herds. Because fertility in the natural mating beef herd is, by definition, the result of dyadic interaction between breeding bulls and estrual females, the observation of such under laboratory conditions would allow formulation of specific hypotheses testable under field conditions. Bulls sexual behavior data obtained utilizing restrained, sedated, nonestrous females only reflects male consummatory rate because it eliminates male and female appetitive behaviors. Failure to elicit or receive appetitive responses from unrestrained, estrual females during pasture mating may be involved with low reproductive efficiency in bulls used in natural mating scenarios.

The following ethological questions bear directly on researchers who have used these methods and also on the testability of assumptions that the bovine female is passive during sexual encounters. What are the specific ways in which we can justify removal of the female's role in "serving capacity" tests when it is commonly a major factor governing sexual activity at pasture? Since formation of the sexually active group in estrous females manifests appetitive behavior in the bull, which could lead to consummatory behaviors, at what point should we deem appetitive behaviors unimportant?

In one of his first dissertation studies, Blockey (1975) was interested in dominance relationships of bulls and how dominance hierarchies affect their sexual activity. Through which maturational process do these dominance relationships develop? Could maternal dominance over the growing bull be directing this coordinating system? To what degree is dominance itself a negative influence on sexual behavior in smaller herds with small numbers of bulls? By suggesting that dominance hierarchies and age among bulls influences their ability to copulate with females, due to agonistic behavior and competition for females, Blockey (1975) should probably have made an effort to design the "serving capacity" experiments to account for this variation. Instead, he ignored that possibility in the pasture mating experiment (Blockey, 1976b),

and placed various aged males together with ovariectomized, estrogenized females at male-to-female ratios of 1:6. This ratio would be considerably less than the 1:20 to 1:30 ratios normally suggested in beef production herds (Spitzer, 1988) and likely maximized the potential for agonistic behaviors, although he suggested it was not an issue (Blockey, 1976b). How might the results have differed if bulls of similar social status were not stratified across receptive females at pasture? How might this have changed the conclusions of the subsequent experiment that led to the development and adoption of the “serving capacity” tests? Are “low serving capacity” bulls always low, regardless of natural mating stimulus conditions?

Beach (1976) and many other ethologists (Tinbergen, 1963; Lorenz, 1970; Agmo, 1999; Pfau, 1996) have provided insight and furthered our understanding of sexual behaviors in animals. Heterosexual copulation has been described as having complex organization of groups of behaviors that involve motivational aspects of learning, experience, and consequences (Bindra, 1974; Agmo, 1999). Copulation requires motivation and motivation may be impeded in one or both partners because of reduced attractiveness of the incentive stimulus, mediated in the bovine through transient postcopulatory intervals, culminating in sexual satiety after many copulations; at times, perhaps bulls can not make the physiological adaptations for intromission and ejaculation, regardless of the abstraction of either “libido” or “mating ability”. Assuming that bull sexual behavior consists of two and only two discrete, context independent components is an example of the reductionism I mentioned earlier, and seems to have inundated the researchers employing restrained, sedated females.

The unrestrained female bovine might develop coordinated motor adaptations, mediated directly through vaginal penetration by the penis, which interfere with completion of repeated copulations. Through lateral or forward movements away from the bull, female bovines could be possibly pacing the rate of copulation. This has little or nothing to do with bull libido or mating ability, yet, could have a dramatic effect on bulls’ “serving capacity”. Receptive females may also recover from sexual satiety and allow further copulations to take place. Perhaps females’ threshold for intromission

during estrus is not only related to the number of copulations previously allowed but also to the number of available mates. Resumption of female sexual behaviors could have a direct affect on the expression of male dominance and could even be a major evolutionary aspect of sexual selection determined by the female (Darwin, 1859).

Perhaps the role that female bovines play in natural selection warrants further consideration. Based upon the work of behavioral ecologists, numerous questions arise regarding sexual selection, sperm competition, game theory and a host of other areas of inquiry. Do bovine females often mate with multiple males during estrus if the opportunity exists? If they do, this would suggest a possible mechanism wherein females influence which males breed. Indeed, as I have already discussed, it is very well established that female cattle are only receptive to intromission during estrus. It is then axiomatic that female bovines exert some control over which males can fertilize their ova, simply by the fact that they control the timing and, perhaps, frequency of copulation during the period of maximal receptivity. This aspect of female sexual behavior has received little, if any, attention thus far in the animal science literature. Potential controlling mechanisms that feedback into the overall mating process, and determine which, and to what extent, gametes are exchanged must be considered with respect to formulating hypotheses. Consideration of sperm competition and game theory appear useful in this regard, yet, have received little to no attention in the field of animal science. On what empirical grounds do supporters of the “serving capacity” tests consider these concepts unimportant in determining overall bovine herd fertility? On what scientific bases to these scientists isolate male consummatory behaviors with inanimate, restrained, sedated females as 1) the standard sexual behavior testing paradigm, 2) the sole important factor of study and 3) analogous to natural mating stimuli?

A complete description of sexual behavior in the bovine utilizing ethological consideration of heterosexual interactions, the nature of sexual activity preference, and the occurrence of such during pasture mating in the bovine is currently not available. Carolyn Merchant (1980), as I suggested previously, outlined the assumptions about

knowledge and the scientific method and are germane in a discussion of some potential reasons as to why there is this present deficit in our knowledge concerning bovine reproductive behavior.

Critique of Conventional Methodology Using Literary Examples of Bias

By utilizing conventional methodology with females restrained in “service crates” investigators have embraced certain assumptions. First, they have made an ontological assumption (Merchant, 1980) in that bovine sexual behavior is comprised of only two discrete parts, that is, male libido and male mating ability. A second assumption embraced by investigators utilizing the conventional approach to quantifying bull sexual behavior is that there is a natural order to the expression of sexual behavior, that is from the hierarchy of precopulatory, copulatory and postcopulatory male typical behaviors (see Figure 1). Thirdly, scientists using the conventional methodology have made an assumption of context independence (Merchant, 1980). Specifically, that knowledge and information about sexual behavior of free-roaming cattle at pasture can be abstracted from allowing bulls to copulate with restrained, sedated females. Under this assumption, bull sexual behavior can be quantified as discrete, sense data that are context independent (i.e. independent of female sexual activity, independent of natural stimuli, etc.).

Hypotheses that would stimulate investigations into factors influencing bull sexual behavior utilizing holistic methodology (e.g. methodology that takes into account the context dependence of male-female interaction, natural mating stimuli, etc.) are greatly needed. Otherwise, there will be continual reassertion of tenuous hypotheses originally directed at eliminating females’ role in overall herd fertility, further limiting our ability to understand female sexual behavior. In my opinion, this practice obfuscates more than it illuminates and represents a major bias in the available research. Below, I attempt to demonstrate this bias by utilizing some of Merchant’s (1980) methods of evaluation.

Merchant (1980) provided numerous literary texts and historical images as evidence of the roots of current environmental dilemmas and cultural biases toward women and

the adoption of mechanistic views of women and nature during the Scientific Revolution. Following her example, I attempt to gain insight into the assumptions underlying conventional scientific investigation of quantifying sexual behavior of bulls. Insight can be gained by examining the discourse (e.g. language) used in the context of such investigations which can reveal both the scientific and nonscientific assumptions that drive research programs. The extent to which nonscientific assumptions predominate in the literature is a measure of bias. Below are just a few examples.

“Bos taurus bulls should be tested using restrained estrous or nonestrous (diestrus) females. It is impractical to use unrestrained estrous cows in serving-capacity tests because successful copulations quickly terminate their sexual receptivity. Behavioral estrus in cows is often terminated following four to eight services, whereas ewes retain their receptivity even when served repeatedly over a period of many hours (E.O. Price, Unpublished Data, 1986).” (from Price, 1987, pg 416).

“The use of restrained, nonestrous cows has nearly all of the advantages of estrous females and almost none of the disadvantages (cost, labor, and number of animals required.” (from Price, 1987, pg. 416).

“Once the bull has detected an oestrous cow it induces it to stand quietly for service.” (from Blockey, 1976a, pg. 388).

“For a period after each service the cow will not stand to be mounted (Wohanka, 1962; Sambraus, 1968). During this period, the sexually active bull restores the cow’s willingness to permit service by vulval sniffing, courtship activity and mounting, in that strict order.” (from Sambraus, 1971; translated and cited by Blockey, 1976a, pg. 388).

“Libido – the willingness and eagerness of a male animal to mount and to attempt service of a female.

Mating Behavior – the behavior of the male animal in the periods immediately before, during and after service.” (from Chenoweth, 1981, pp. 155-156).

“Single-sire breeding, while potentially more efficient than multi-sire breeding, is dependent upon the reproductive capabilities of the sire.” (from Chenoweth, 1981, pg. 155).

“Bulls of low serving capacity displayed poor fertility, having a significantly lower conception rate ($P < 0.0001$) and pregnancy rate ($P < 0.0001$) than bulls of medium or high serving capacity.” (from Blockey, 1989, pg. 350).

“...Thus, use of [restrained] females in estrous would appear unnecessary to test libido or serving capacity in bulls provided the stimulus females employed are properly restrained and presented. This supports the observation (Blockey, 1975) that immobility of the female is the greatest single stimulus to a bull to complete service.” (from Chenoweth, 1979, pg. 228).

“The greatest single stimulus to a bull to mount and attempt service is immobility of the female (Blockey, 1975; Chenoweth et al., 1979). Physiological estrus is not necessary for the bull to attempt mounting and service, providing adequate immobility is displayed (Chenoweth et al., 1979). A suitable stimulus need not even be female (Amann et al., 1976) confirming that an inverted “U” shape is the visual configuration most stimulatory to the release of mounting behavior in bulls (Boissou, 1975).” (from Chenoweth, 1983, pg. 174).

“The heifers were restrained in service crates. As soon as a heifer became unreceptive she was replaced by another.” (from Crichton and Lishman, 1985, pg. 23).

“The ejaculation is the culmination point of copulation and, after achieving sexual satisfaction the behaviour of the male changes completely. Sexual drive and sensitivity to sexual stimuli disappear for some time in the animal. It seems as if the ejaculation releases the copulative energy.” (from Wierzbowski, 1966, pg. 66).

From these passages, one could formulate certain hypotheses, using the assumptions embraced by these investigators. Below, I provide a few examples.

Present Hypotheses Concerning Bull Sexual Behavior Utilizing Conventional Methods

First, the motivation and physical expression of mounting behavior in the bull is controlled by the males' innate, sexual drive (i.e. libido) and mating ability (i.e. the ability to copulate), both of which somehow coordinate and interact to instigate mounting when bulls perceive an immobile, inverted "U" shaped object. Second, restraining teaser females provides the most favorable natural stimulus condition for bulls, allowing them to express their natural, innate level of sexual behavior. This occurs because the conventional methodology eliminates other time-consuming behaviors (i.e. courtship, mounting of the male by the female, etc.) and also eliminates females' ability to terminate copulation after successful "services". Thirdly, the bull is the most active partner in heterosexual mating because during copulation he induces the female to stand "quietly" for the "service" and, afterwards, restores her willingness to copulate further. Furthermore, ejaculation by the male is seen as a release of copulatory energy, of which the female has none.

While all of these views embrace androcentricism and dualism, the latter view has been persistent in scientific discourse for more than 2000 years, perhaps originating with Aristotelian biological theories (Merchant, 1980). Aristotle viewed the female as an incomplete male since the coldness (i.e. inert matter) of the female would not allow menstrual blood to perfect itself as semen (Merchant, 1980). In terms of generation of new offspring, Aristotle believed that the male was the real "cause" of embryos as he suggested,

"The female, as female, is passive and the male, as male, is active, and the principle of movement comes from him" and "...only makes a living creature by the power which resides in the semen." (Aristotle, ca. 335-322 B.C., cited by Merchant, 1980, pg. 13).

As Merchant (1980) goes on to suggest, most sixteenth and seventeenth century authors of science embraced Aristotelian views of female passivity, allowing these views to become thoroughly entrenched in society by the eighteenth and nineteenth centuries. One such author, William Harvey, who made groundbreaking discoveries associated

with mammalian blood circulation, made several androcentric claims about the dualism of female passivity, male activity. Male power, through his active semen, he suggested, was the causative source of reproductive energy (Merchant, 1980). For example, he wrote,

“...I, for my part, greatly wonder how anyone can believe that from parts so imperfect and obscure [as the genital organs of the woman], a fluid like the semen, so elaborate and concoct, and vivifying, can ever be produced [by the female], endowed with force and spirit and generative influence adequate to overcome that of the male...how should such a fluid as the male semen be made to play the part of mere matter?”; (Harvey, 1847, cited by Merchant, 1980, pg. 159)

Based upon this analysis of the discourse used in describing the female bovine in the mating process and the similarity of this discourse to culturally biased, androcentric assumptions which have been insidious in science for millennia, I suggest that the nonscientific assumptions associated with conventional methodology investigating bull sexual behavior are also inundated with these biases. By evaluating these passages, one could hypothesize that it is accepted practice to restrain bovine females because they are viewed as mere objects *detering* males' inherent sexual prowess. Not only is this contradictory to an ethological approach to studying sexual behavior, this conventional view seems inconsistent with its own assumptions. That is, females are viewed as being passive in the reproductive process and, yet, they interfere with the innate expression of male sexual behavior. This appears to be a major conundrum. Below, I provide some alternative discourse and hypotheses concerning the sexual behavior of bulls, utilizing an ethological framework while attempting to circumvent these presently held, nonscientific assumptions which seem biased.

Toward Novel Hypotheses Concerning Sexual Behavior of Bulls

An ethological approach to studying sexual behavior might allow us to formulate novel hypotheses concerning reproductive behavior in the bovine utilizing pluralistic assumptions of male and female perspectives. For example, bulls and estrual females copulate in a dyadic interaction involving the expression of appetitive and

consummatory behaviors expressed by both the bull and the estrual female. After several copulations, both the male and female will cease being receptive to sexual activity, perhaps more transiently in the bull. Hence, this postejaculatory interval could be sexually dimorphic in intensity and (or) duration, whereas, sexual satiety in both the male and the estrual female can be overridden by provision or encounter of a novel, attractive sexual partner.

Additional hypotheses could be constructed concerning variation in sexual behavior among and within individual bulls. For example, bull sexual behavior, as an interaction between the bull's libido, mating ability, and interactive sexual stimuli, is expressed upon attainment of appropriate mating context and learning. Behavioral patterns of bulls' sexual behavior may be important in governing the rate and extent to which partners in heterosexual dyads copulate. For example, some bulls may express intromissions in a high frequency, short duration mode while others express them in a low frequency, long duration pattern. Perhaps sexual behavior patterns are expressed in a completely random fashion, owing only to physiological aberrations and recovery. How would we know the extent to which the expression of patterns bull sexual behavior influence beef female conception rates when the status quo has been to utilize restrained females?

We could also hypothesize that using unrestrained, estrual females in bull sexual behavior tests represents a reasonably close approximation to natural mating stimulus conditions (i.e. stimuli the bull will encounter during a pasture mating scenario) such that bulls will express quantifiable behavior with females of varying stimulus conditions (e.g. estrual, nonestrual, females that allowed previous intromissions, etc.). Close observation of such behaviors and dyadic interaction in a laboratory setting would provide data which could be statistically analyzed to help develop hypotheses that are testable and falsifiable under field conditions. I should mention that other researchers have used unrestrained females in sexual behavior tests (Chenoweth et al., 1979; Boyd and Lunstra, 1989; de Araujo et al., 2003) and previous research from this laboratory suggested that restraint of females was not necessary to effectively quantify

mounting activity of bulls (Smith et al., 2000; Bailey et al., 2002; Imwalle and Schillo, 2002). By developing these, and other, hypotheses, new research questions can be asked about other factors that could influence sexual behavior in the bull and ultimately endeavors to understand how these parameters can influence beef herd fertility. In addition to being critical of the conventional methodology from both an ethological perspective and from a biased methodological perspective, one should certainly mention that restraining females in “serving” crates creates a risk associated with animal injury as well as basic animal welfare concerns.

Critique of Conventional Methods from an Animal Welfare Perspective

In addition to methodological concerns associated with the conventional approach, one could certainly question the practice of severely restraining and sedating teaser females from an ethical standpoint concerned with animal welfare. One researcher called the practice of restraining females during “serving capacity” tests inhumane and in violation of animal protection acts of New Zealand. In fact, it prompted the veterinary officer to write a letter to the New Zealand Veterinary Journal at how appalled the citizenry and he were after witnessing the “serving capacity” test at an agricultural exposition.

“...Details of the test were given in [a previous publication], but briefly it consists of having three or four anoestrus heifers restrained in a large yard and allowing up to 20 sexually stimulated bulls to mount them repeatedly for up to 40 minutes. [At this event], “three small yearling heifers restrained by the head and having a post in the ground at each shoulder to minimize lateral movement were repeatedly raped by five or six mature bulls until two of them collapsed, bleeding from the vagina. They were “helped” to their feet by a combination of tail twisting and kicking to face another onslaught by a fresh group of bulls.” (from a letter by D. Fraser, 1983; 31:20, *Letters to the Editor, New Zealand Veterinary Journal*).

In an accompanying letter, another veterinary officer was asked to respond to Fraser's (1983) comments. Packard (1983) suggested in his own letter to the editor that Fraser's and the citizens' concerns were unfounded. Fraser (1983) writes,

"It is true that a couple of the heifers being restrained did 'get down' but this was due to the inadequacies of the restraint method used and the size of the heifers...It is also true that one heifer did show signs of bleeding during the test. At that point the test was stopped and she was inspected by the veterinarian present before the test was allowed to resume." (from a letter by P. M. Packard, 1983; 31:20, *Letters to the Editor, New Zealand Veterinary Journal*).

Packard (1983) further claimed, "how emotive people viewing these tests can become if the incorrect procedures or information is not understood by all concerned," which would seem to suggest 1) ethical concerns about the welfare of experimental animals are solely based on emotions and 2) that people concerned about these procedures do not possess an aptitude or understanding of science. What could be more scientific than critically questioning the underlying methodological assumptions that scientists use to gain insight into their hypotheses through their *practices* in science?

Summary of Critique

The inadequacy of hypotheses about bull sexual behavior supported by certain conventional assumptions (i.e. bulls' sexual behavior is controlled solely by their own innate, sexual libido and mating ability independent of the female) is illustrated by considering an ethological perspective of studying sexual behavior. For example, consideration of the interactions among male and female appetitive and consummatory behaviors, individual bull integration into the sexually active group, dynamics of the formation of the sexually active group, and female preferences for certain males of differing attractiveness are all aspects of bovine sexual behavior to which hypotheses could be formulated, tested, and falsified or accepted.

Development of these hypotheses could lead to management practices that could impact beef herd fertility and, eventually, producer profitability. These potential areas of research have never been discussed completely in the literature associated with

reproductive behavior of cattle. By basing behavioral models on a unitary assumption (i.e. “serving capacity” of bulls toward inanimate, restrained females predicts overall pasture fertility) rather than interactions involving free-roaming animals, Blockey (1975) and those who utilize restrained females have inadvertently embraced reductionistic conclusions regarding the control of sexual behavior in the bull and its impact on beef herd fertility. New approaches to understanding bovine sexual behavior must endeavor to acknowledge this complexity and emphasize those areas of uncertainty in order to gain insight into how behavior ultimately affects beef herd fertility. This critique was written under my belief that such approaches will contribute to research that will allow us to become more informed about this very topic.

Final Summary and Conclusions

My goal with writing this review of literature was to establish new discourse on the existing testing paradigms commonly employed by researchers studying sexual behavior of bulls. In addition, I endeavored to utilize an interdisciplinary approach to understanding other traditional approaches to studying behavior. By utilizing ethologist descriptions of dyadic heterosexual mating and by relying on Carolyn Merchant’s methods of inquiry concerning androcentric bias and assumptions in science, I asked new questions about the control of sexual behavior in the bovine; questions that could lead to new hypotheses and, ultimately, a novel theory about the oscillating, interactive process of mating in this species.

I also discussed how the principals of ethology are intertwined within the concepts of the adaptive theory of behavior. This theory suggested that neural processes, dependant on gonadal steroids and neurotransmission, promotes goal-directed actions in relation to particular classes of incentive stimuli which have had some impact on reinforcing the individual, providing sexual context and experiences with consequences. In this model, there is a mutually exciting relationship between the incentive stimulus partners which interleaves the ethological concepts of sexual behavior with basic physiology, psychology and genetics. I made considerable effort suggesting that the intricacies of the proposed models revealed the underlying

neuroendocrine and endocrine bases for sexual motivation. I suggested, through consideration of the original work of ethology, that enhancing the sensory system's responsiveness to sexual stimuli excites the central motive state, which represents system reciprocity and functions as a positive feedback system.

I suggested that this positive feedback could lead to the consummatory phases of copulation and, in the case of the bovine, would interplay among distinct bouts of dyadic copulation, eventually leading to periods of postejaculatory inhibition of behavior, and finally sexual satiation. I discussed one theory, the Coolidge Effect, which described the reinitiation of appetitive and (or) consummatory behaviors in sexually satiated animals that are immediately exposed to novel, receptive partners.

Traditional approaches to studying sexual behavior of the bovine have embraced techniques that are questionable from a scientific, methodological, and ethical standpoint. In these studies, females were usually severely restrained, injected with tranquilizer, and received copious amounts of lubricant to the vagina to reduce chafing. Bulls are usually tested in groups whose members outnumber those of the females' to induce competition. The females used in these tests are reduced to inverted, U-shaped objects wherein females do not even need to be in estrus to conduct these tests. I questioned the validity of the assumptions associated with the use of severely restrained, sedated, nonestral females. Although some researchers have embraced the unrestrained female models, there are too few examples that have employed extensive and repeated testing of these subjects especially under varying female stimulus conditions.

The key assumptions associated with my new, working hypothesis are related to an ethological approach to studying sexual behavior in the bull. First, bulls will express quantifiable sexual behavior with unrestrained, estrual females in small pens. Further, I assume that a testing paradigm of this type represents a reasonably close approximation to natural mating stimulus conditions (i.e. stimuli the bull will encounter during a pasture mating scenario). This assumption embraces the ethological concepts of a highly interactive, dyadic mating process where the male and female are

both equally involved. Second, the expression of bull sexual behavior will be dramatically altered with females of varying stimulus conditions (e.g. estrual, nonestrual, novel, familiar, etc.). A third assumption is that variation in bull sexual behavior is larger among bulls than within the same bull across several behavior tests. Thirdly, close observation and repeated testing of male and female sexual interaction in a laboratory setting will provide information to help develop hypotheses that are testable and falsifiable under field conditions.

In the first experiment, I wanted to know if I could observe adequate male behavior using unrestrained females. In addition, I also wanted to gain insight into what stimulus conditions associated with the female would be most conducive to sexual behavior expression. I tested the hypothesis that female novelty and receptivity influences the expression of appetitive and consummatory responses in the bull. By periodically changing the stimulus female and replacing her with a novel stimulus female, I would be able to demonstrate the degree to which bulls maintain sexual activity when presented with novel, receptive stimuli. Simply replacing the original female back in the testing pen would allow me to demonstrate sexual satiety in the bull from a temporal perspective. Using a female that is nonreceptive to intromission by the male would provide the appropriate negative control and allow me to determine temporal characteristics of motivation when bulls are not allowed intromission.

In the second experiment, I examined the temporal characteristics of sexual behavior in a group of bulls tested repeatedly with different exposure patterns with unrestrained, receptive females. I wanted to know whether bulls show a different pattern of sexual behavior when allowed access to several estrual females sequentially or as a group during the same temporal period. In addition, I wanted to determine the threshold of receptivity in the females who were repeatedly allowed access to different male partners. I tested the hypothesis that bulls would express greater appetitive and consummatory sexual behaviors during tests when they are exposed to a small group of unrestrained, estrual females. I also hypothesized that female bovine would allow mounting and copulation with more than one male during behavioral estrus. Bovine

females, I further hypothesized, would show a dramatic decrease in their willingness to allow mounting and intromission by males but would not entirely cease copulating with novel males during the testing periods.

Chapter Two

The Effects of Female Novelty and Receptivity on the Expression of Sexual Behavior in Adult Male Bovine

Introduction

Although the sexual behavior of bulls is well defined and various approaches have been developed to quantify behavioral components of the sexual efficiency of bulls (Blockey, 1975; 1976a,b,c; 1981 a,b,c; 1989); Lunstra, 1986; Boyd et al., 1989), few studies have focused on the mechanisms regulating this behavior (Imwalle and Schillo, 2002). The use of “serving capacity” tests (Blockey, 1976b; 1981a,b,c; 1989; Chenoweth, 1981; Christensen, et al, 1982; Lunstra, 1986; Price, 1987), which are the predominant tests for assessing sexual behavior of bulls, embrace methodologies that remove the female as an active participant in behavioral interactions that culminate in copulation. Although some researchers have used unrestrained bovine females in testing paradigms (Dykeman et al., 1982; Katz and Price, 1986; Carpenter et al., 1992; Jago et al., 1997; de Araujo et al., 2003) variable female stimulus conditions effects on the expression of sexual behavior in the bull have not been extensively studied. Moreover, existing tests of sexual behavior may not accurately assess a bull's sexual behavior under field conditions, and such tests often produce results too variable for testing hypotheses about regulation of sexual behavior (Price, 1987). For example, short-term tests of serving capacity (5-10 min.) have resulted in low correlations between “serving capacity” scores and pasture pregnancy rates ($r=.09$, Chenoweth, 1978; $r=.32$, Sullins et al., 1979). With this background in mind, this experiment was designed to develop a reliable method for assessing sexual behavior of bulls and to employ this approach to address fundamental questions concerning female stimulus conditions in the regulation of sexual behavior in bulls.

“Serving capacity” tests involving severely restrained teaser females may not permit full expression of bull sexual behavior and may be considered inhumane if the ratio of males far exceeds that of the females (Price and Wallach, 1991a). Methods that involve unrestrained females have been developed, but it is unclear how long such tests should last and how many females should be involved in order to optimize expression of bull sexual behavior. Moreover, based on our initial experiences with such tests, it appeared that the presence of investigators can interfere with expression of copulatory behavior. Using a remote surveillance system employing procedures that utilized unrestrained, estrual females as stimulus animals in behavior tests conducted in small pens would allow us to, 1) evaluate the use of surveillance cameras and video recording equipment to monitor and quantify mating behavior of bulls; 2) determine if repeated exposure of bulls to novel, estrual females enhances expression of mating behavior compared to sequential exposure to a familiar estrual or diestrual female. The objective of this experiment was to evaluate the effects of repeated exposure to females varying in novelty and receptivity on the expression of sexual behavior in adult, sexually experienced bulls.

Materials and Methods

General

This experiment consisted of three replicates (Replicate 1, Replicate 2, and Replicate 3, respectively) of a Latin Square Design with repeated measures. Replicate 1 was conducted between December, 2001 and February, 2002, Replicate 2 was conducted between March, 2002 and May, 2002, and Replicate 3 was conducted during November, 2002. All procedures were conducted at the University of Kentucky Animal Research Center in Woodford County, KY. All experimental procedures on animals were approved by the University of Kentucky Institutional Animal Care and Use Committee.

Males

In each replicate (n=3), 4 Black Angus bulls were randomly chosen from larger contemporary groups who had been reared and housed together. Bulls in Replicate 1

and 2 were all born between March and April, 2000, whereas, bulls in Replicate 3 were born between March and April, 2001. Bulls in all replicates either had previous sexual experience (Replicates 2 and 3) or were provided opportunities to mate with ovariectomized, estrogenized females; the latter procedure also allowed us to familiarize ourselves with the surveillance equipment and verify that different categories of sexual behavior could be identified.

At the beginning of each replicate, the mean \pm SEM age of bulls in Replicates 1, 2, and 3, were 634 ± 14 , 726 ± 4 , and 592 ± 22 days, respectively. When comparing the age of the bulls at the start of their first behavior tests, bull ages between replicates were different ($P < 0.01$), with bulls in Replicate 2 being oldest followed by bulls in Replicate 1, who were older ($P < 0.01$) than bulls in Replicate 3.

Mean (\pm SEM) body weights of the bulls in Replicates 1, 2, and 3 (measured at the beginning of each replicate) were 557 ± 17 , 669 ± 9.9 , and 574 ± 13 kg, respectively. Bulls in Replicate 2 were significantly heavier ($P = 0.002$) at the start of behavior tests than bulls in Replicates 1 and 3, who had similar ($P > 0.10$) body weights.

All bulls in Replicates 1 and 3 were kept as a group in pastures (6.07 hectares) with *ad libitum* access to water and forage while receiving periodic access to a supplemental protein, energy and trace mineral ration. Bulls in Replicate 2 were maintained as a group in an open-sided barn within pens (approximately 4 m X 20 m) with bedding material on a concrete floor. Bulls in Replicate 2 received *ad libitum* access to the ration, consisting of corn silage, protein, and mineral supplement, fed once per day in concrete bunks at one end of the pen. All bulls were fed diets designed to meet National Research Council requirements for mature bulls (NRC, 1996). During the behavior tests animals did not have access to food or water.

Before conducting each replicate, all bulls had been subjected to a standard breeding soundness exam (Spitzer et al., 1988) performed by a licensed veterinarian. The breeding soundness exam is designed to evaluate the general physical condition of the bull; in addition a sample of semen is collected via electroejaculation to assess sperm quality (e.g. overall sperm motility and gross morphology). The purpose of this exam is

to establish a general idea of a bull's potential as a breeding member of the herd. All bulls used in this experiment were deemed acceptable for breeding based on these criteria.

Females

A small group of 10 crossbred, intact, nulliparous females were chosen from a larger group of females (n=30). The same 10 females were used for both Replicates 1 and 2. The 10 females were chosen based on homology of ovarian structures (determined by transrectal ultrasonography) and synchrony of estrus within 48 hours following intramuscular (i.m.) injection of 5 mL (25 mg prostaglandin F_{2α}) of Lutalyse® (Pharmacia & Upjohn, Kalamazoo, MI). Females used in Replicates 1 and 2 were born between March and April, 2000, making them approximately 21 months of age at the start of Replicate 1 and 24 months of age at the start of Replicate 2. Exact birth records were not available.

A larger group of intact females was available to use in Replicate 3. Sixty-seven predominantly Black Angus females were stratified into three herds (n=22, 22, and 23, respectively) based on synchrony of estrus within 24-48 hours following intramuscular injection of Lutalyse® followed by an i.m. injection of estradiol cypionate (Pharmacia & Upjohn, Kalamazoo, MI). Females used in Replicate 3 were of various ages ranging from 20 months to 9 years of age, however, the exact dates of birth were unavailable.

Mean (\pm SEM) body weights of the females in Replicates 1, 2, and 3 (measured at the beginning of each replicate) were 442 ± 11 , 551 ± 20 , and 508 ± 24 kg, respectively. Females in Replicate 1 were significantly lighter ($P < 0.01$) at the start of behavior tests than females in Replicates 2 and 3, who had similar ($P > 0.10$) body weights.

All females were maintained on pasture (6.07 hectares) at the University of Kentucky Animal Research Center, Woodford County, Kentucky, with *ad libitum* access to water and forage while receiving periodic access to a supplemental protein, energy and trace mineral ration designed to meet National Research Council requirements for nonlactating, mature beef females (NRC, 1996).

Estrus Induction for Sexual Behavior Tests

Females received an injection of Lutalyse® 12 to 15 days after the first observed estrus induced during the previous ultrasonography and selection period. Approximately, 24 hours later, females were injected with 0.5 mL (1 mg) of estradiol cypionate to induce behavioral estrus. At random, one female, serving as the diestrus stimulus animal for treatment D, did not receive the injections.

This induction protocol induced estrus approximately 16-36 hours after estradiol cypionate administration for approximately 12-16 hours which is in close agreement with the research of Pancarci et al. (2002). In a large observation pen (29.6 m X 3.7 m), before the sexual behavior test began, females were visually examined for signs of standing estrus and only heifers in estrus were used as stimulus females in treatments A, B, and C, respectively. Criteria for standing estrus included mounting and standing firm to a mount, indicated by no lateral or forward movement after being mounted.

In this experiment, the protocol consistently induced estrus between 26-32 hours after estradiol injection in 85-95% of the females injected. Diestrus females refused to stand firm to homosexual mounts in every instance and in most instances, did not mount other females in estrus. Immediately after behavior testing, the female used as the diestrus stimulus in treatment D received an injection of Lutalyse® to maintain synchronous cyclicity with the other female herdmates.

Behavior Test Procedure

In each replicate, bulls were randomly allotted to treatments (n=4) based on a randomly chosen Latin Square arrangement (Snedecor and Cochran, 1980). The bulls were exposed individually to each female at a 1:1 male to female ratio for approximately 60-minutes in the following treatments. Treatment A - sequential exposure to 4 estrual heifers; Treatment B - alternating exposure to 2 estrual heifers; Treatment C - sequential exposure to 1 estrual heifer; and Treatment D - sequential exposure to 1 diestrus heifer.

There were four testing days within each of the three replicates. Nested within each test day and treatment combination there were 4, 60-minute sexual behavior tests. The

bulls were exposed to one treatment each day, depending on the Latin Square arrangement. In Replicate 1, the interval between the 4 test days was 14, 17, and 17 days, respectively. For Replicate 2, the interval was 15, 17, 14 days, respectively. Variation in the testing intervals was based on forecasted weather. Attempts were made to reduce possible inclement weather effects on sexual behavior by testing during days where snow or rainfall was not probable. In Replicate 3, since we had access to 3 herds of females, this allowed testing behavior more often with a larger number of females, resulting in a much shorter, 4 day testing interval.

Bulls in Replicates 1, 2, and 3 were tested between December 20, 2001 and February 8, 2002, March 18 and May 8, 2002, and November 4 and November 16, 2002, respectively. Behavior tests for Replicate 1, 2, and 3 were conducted between 1500 h and 0400 h, 1500 h and 0100 h, and 1300 h and 2300 h, respectively. For Replicates 1,2, and 3, ambient air temperatures on testing days, during these specific times, ranged from -13°C to 20°C, from 0.5°C to 25°C, and 2°C to 14°C, respectively.

On test day, all bulls were given the opportunity to become stimulated by visually observing homosexual mounting activity of the females occupying the large observation pen. Smaller, adjacent pens (7.4 m X 1.85 m) were used to confine each bull individually during its pre-test stimulation period. Bulls could investigate females in the observation pen by placing their noses through the cross bars on the gates, sniffing or licking females. Bulls often had protruding penises during the prestimulation period wherein they often exhibited pre-ejaculatory emissions (not quantified). The flooring in the observation pen was fine gravel whereas the flooring in the adjacent, stimulation pens was concrete.

Females in the adjacent observation pen continually traversed it, exhibiting homosexual mounting, attempted mounts and chin-rests; at times, females investigated the bulls by placing their noses through the crossbars on the gates and, again, either sniffing or licking the male. The pre-stimulation period lasted at least 30 minutes. When the necessary number (n=7) of estrual females were determined to be in standing estrus, females were removed from the large observation pen and placed in an adjacent

holding pen, still separated from the bulls. Gates within the large observation pen were then closed and firmly latched, resulting in 4 testing pens of equal size (7.4 m X 3.7 m) separated by the individual gates. Bulls were then allowed into testing pens wherein the bulls' ID numbers and pen locations were recorded and cross referenced to the randomized Latin Square arrangement. Estrual stimulus females were then randomly allocated within the pretest observation pens; the nonreceptive diestrus female was then located adjacent to the appropriate bull. At this point all animal ID numbers were meticulously recorded and cross referenced. Once the arrangement was verified, the video equipment was set to record all events in all pens simultaneously on one video cassette tape, and the test was begun. Females were placed in the appropriate pen with the specific bulls at a 1:1 ratio and removed after approximately 60-minutes, regardless of treatment. Females were reintroduced to the bulls after approximately 2-4 minutes and the second hour test was begun. This procedure was followed until the end of the behavior testing procedure. Figure 6 diagrams the testing apparatus for a hypothetical testing day.

Sexual behavior of bulls was monitored by four video surveillance cameras. Each camera was positioned to provide a complete, individual view of each of the four test pens. During the test, activity in these areas was recorded on video tape using a duplex-multiplexer and a 24-hour, real-time video cassette recorder. This equipment permits simultaneous viewing of all four test pens and provides a method of both removing possible handler effects while providing a way to closely scrutinize and quantify specific behavioral categories. When the observer noted an event, the duplex multiplexer was changed from the quad-camera mode (i.e. the mode showing all four pens at once) to the specific reference camera mode (i.e. a single screen showing only the specific pen). After reviewing and recording a particular behavior, the tape was then rewound and the behavioral events viewed and reviewed as necessary. The video cassette timer, which was set to local time, exhibited hour, minutes, and seconds in the format hh:mm:ss; these times were used for denoting when particular behaviors occurred. In addition, 4 column analyses pads were used to keep records of each

behavioral event. One single sheet was used for each bull x treatment x replicate combination, delineated by hours. New sheets were made for each behavior test day. Once the behavior was recorded, the tape was then rewound at least 15 seconds previous to the last event, placed back into quad mode, and further viewing commenced.

Tapes were examined by one observer and the following behavioral traits were quantified; numbers of mounts with intromission, aborted mounts (i.e. mounts not culminating in intromission), and flehmen responses, respectively. We did not differentiate between mounts with intromission with or without a final, deep pelvic thrust. Calculations were also made concerning the temporal characteristic of mounting interval (i.e. mean time between mounts, with or without intromission). Any event wherein the bull raised both front feet off of the ground and directed his movement toward a female was termed a mount. A mount with intromission was defined by the bull mounting the female dorsally and from the rear with penile intromission, followed by pelvic thrusting. An aborted mount was defined as any mount in which the bull failed to have intromission (i.e. mounting the female's head, flanks, or rear with no intromission or thrusting). A flehmen response was defined as a flexing of the nostrils nearly ninety degrees, deep breathing and a lifting of the upper lips after investigation of the female's anogenital, flank, or rear leg areas.

When viewing the video tapes, occasionally, based on the angle of the male and female, penis insertion could not be verified. On these rare occasions, if the male was seen thrusting upon the female's rear and exhibited a final, deep pelvic thrust, the event was classified as a mount with intromission; if the male mounted the female's rear, but no thrusting occurred, it was classified as an aborted mount.

Statistical Analyses

The design of this experiment was a replicated Latin Square with repeated measures. Because special analyses are required for this type of data, standard regression and analysis of variance methods may produce invalid results because of mathematical

assumptions that may not hold under complex covariance structures associated with the autocorrelated data (Littell et al., 1998). Hence, we chose to use the techniques of Littell et al. (2000) to account for these concerns and model the appropriate covariance structure within each dependent variable. Dependent variables, recall, were numbers of total mounts, mounts with intromissions, aborted mounts, mean mounting interval, and numbers of flehmen responses, all taken from the 4, 60-minute behavior tests for each individual bull each test day within each replicate.

These data were subjected to analysis of variance using the PROC MIXED procedure of the Statistical Analysis System (SAS, v. 8.02, Institute, Cary, IN). The models contained fixed effects for treatment, time (i.e. hour nested within day), test day, and replicate, in addition to the interactions of treatment x time, replicate x time, treatment x replicate, test day x time, and treatment x time x replicate. Data were modeled using animal within treatment as random subject effects and replicate was used as a random group effect; both effects were included in the model to account for possible between subject heterogeneity (Littell et al., 2000). Using the techniques of Wolfinger et al. (1996), a first order autoregressive, heterogeneous covariance structure was selected to account for the within-animal correlations for all longitudinal data associated with our dependent variables, except for mounting interval, where a compound symmetrical covariance structure fit best. Least square means procedures were used to calculate means and standard errors in addition to statistically comparing (pairwise) all significant fixed effects and their interactions.

We were interested in determining if the expression of sexual behaviors among treatments were temporally changing, hence, an analysis was performed fitting the treatment regressions on a set of orthogonal polynomials in time up to degree three (thus, a complete set of contrasts for the differences among the four levels of time), and their interactions with the stimulus female treatments. Contrast statements were then included to request tests of linear, quadratic, and cubic, effects of time within each treatment.

One bull (ID # K109) in Replicate 2 displayed aggressive behaviors toward all females he was exposed to. These included excessive head butts to the females' head, flanks, and rear. In addition, he spent most of the test time standing on gates attempting to jump into other pens. Excessive male-male aggressive encounters were instigated by this bull outside of testing periods. He never exhibited any sexual interest in females except for 4 flehmen responses the first test day. I chose to eliminate this bull from all statistical analyses.

Results

Total Mounts

The analysis of variance for total mounts (i.e. mounts with intromission plus aborted mounts) indicated that treatment, time, and the treatment x time interaction were all significant ($P < 0.01$).

When averaging across the 4, 1-hour behavior tests, replicates and test days, least square mean total mounts were similar ($P > 0.10$) when bulls were in Treatment A, B, and C but were greater ($P < 0.001$) when compared pairwise to when bulls were in Treatment D. Least square mean (\pm SEM) total mounts for Treatment A, B, C, and D were 6.6, 6.3, 5.3, and 1.4 ± 0.8 total mounts•bull⁻¹•treatment⁻¹, respectively).

Least square total mounts decreased over the 4, 1-hour behavior tests in a quadratic fashion. Least square total mounts (\pm SEM) for the 4, 60-minute behavior tests were 7.9 ± 0.8 , 4.4 ± 0.7 , 3 ± 0.5 , and 4.3 ± 0.8 total mounts•bull⁻¹•hour⁻¹, respectively. Least square mean total mounts were greater for the 1st hour than for all subsequent hours of testing periods. Similarly, least square mean total mounts for the 2nd 60-minute test period were greater ($P = 0.05$) than least square mean total mounts during the 3rd hour test period but were not different ($P > 0.10$) than total mounts during the 4th hour of testing. Least square mean total mounts were similar ($P > 0.10$) during the 3rd hour of behavior testing when compared to those during the 4th hour of testing.

The treatment by time interaction for total mounts is shown in Figure 7. During the first hour, total mounts (\pm SEM) were similar ($P > 0.10$) when bulls were in Treatments A, B, or C ($8.6, 11, \text{ and } 10 \pm 1.5$ total mounts•bull⁻¹•hour⁻¹). In addition, when bulls were

in Treatment D, there were fewer ($P < 0.05$) total mounts (\pm SEM) (2.2 ± 1.5 total mounts•bull⁻¹•hour⁻¹) when compared pairwise to when they were in other treatments. During the second hour, more total mounts were exhibited by bulls when they were in Treatment A and B (7 and 6.9 total mounts•bull⁻¹•hour⁻¹, respectively) versus both Treatment C and D (3.1 and 2.2 total mounts•bull⁻¹•hour⁻¹, $P < 0.05$, respectively; SEM = ± 1.2 mounts with intromission•bull⁻¹•hour⁻¹). Total mounts were similar ($P > 0.10$) when bulls were in Treatments C and D during the second hour. During the third hour of testing, total mounts (\pm SEM) were similar ($P > 0.10$) among treatments A, B, and C (2.9, 3.5, and 4.5 ± 1 total mounts•bull⁻¹•hour⁻¹, respectively); Treatments A and B were similar ($P > 0.10$) to Treatment D (1.3 total mounts•bull⁻¹•hour⁻¹), whereas, total mounts were higher ($P < 0.05$) in Treatment C compared to D. During the final hour of testing, when bulls were in Treatment A, they exhibited more total mounts (\pm SEM; $P < 0.05$ in all cases) compared to when they were in the other treatments (8.1 versus 3.8, 3.7 and 1.7 ± 1.5 mounts with intromission•bull⁻¹•hour⁻¹, respectively). Total mounts were similar ($P > 0.10$) when bulls were in Treatments B, C, and D during this time.

Tests for linear, quadratic, and cubic, effects of time within each treatment suggested the following. Total mounts in Treatments A and C changed across time in a cubic fashion ($P < 0.001$ and $P = 0.06$, respectively) whereas total mounts decreased in a linear manner ($P < 0.03$) when bulls were in Treatment B. No regression line ($P > 0.10$) could be fit to the data associated with Treatment D.

Mounts with Intromission

As we expected, when bulls were sequentially exposed to receptive females, regardless of novelty, (Treatments A, B, and C) they exhibited more mounts with intromission than when sequentially exposed to a diestrus female (Treatment D) (3.7, 3.6, 2.3 versus 0 ± 0.5 (SEM) mounts with intromission•bull⁻¹•treatment⁻¹). Total mounts with intromission, when averaged across the 4 hours, tended to be greater when bulls were in Treatments A or B (3.7 and 3.6 mounts with intromission •bull⁻¹•treatment⁻¹, respectively) versus when they were in Treatment C (2.3 mounts with

intromission•bull⁻¹•treatment⁻¹, $P = 0.06$ and $P = 0.08$, respectively). Least square mean mounts with intromission averaged across time were not different (3.7 and 3.6 mounts with intromission•bull⁻¹•treatment⁻¹, $P > 0.10$) when bulls were in Treatment A versus Treatment B.

The fixed effect of time was significant ($P < 0.0001$) with respect to mounts with intromission. Averaging across all treatments, days and replicates, mounts with intromission decreased in a quadratic fashion ($P = 0.005$) across the 4, 60-minute behavior tests. Least square mean (\pm SEM) for mounts with intromission for 60-minute behavior tests 1, 2, 3, and 4 were 4.1 ± 0.6 , 2.6 ± 0.4 , 1.1 ± 0.31 , and 1.8 ± 0.4 mounts with intromission•hour⁻¹, respectively. Mounts with intromission were higher ($P < 0.02$) during the first hour when compared pairwise to all subsequent hours of testing. In addition, mounts with intromission during the second hour of testing were significantly higher ($P < 0.01$) than mounts with intromission during the third hour of testing but were similar ($P > 0.20$) to the number of mounts with intromission during Hour 4. Mounts with intromission were similar ($P > 0.10$) between Hours 3 and 4, when compared pairwise.

The treatment by time interaction for mounts with intromission is shown in Figure 8. Obviously, bulls in Treatment D never exhibited mounting with intromission. During the first hour, mounts with intromission were similar ($P > 0.10$) when bulls were in Treatments A, B, or C ($5.4, 5, 6.1 \pm 1.2$ (\pm SEM) mounts with intromission•bull⁻¹•hour⁻¹). During the second hour, more mounts with intromission were exhibited by bulls when they were in Treatment A and B (3.7 and 5.4 mounts with intromission •bull⁻¹•hour⁻¹, respectively) versus Treatment C (1.1 mounts with intromission•bull⁻¹•hour⁻¹, $P < 0.025$ and $P < 0.01$, respectively; SEM = ± 0.8 mounts with intromission•bull⁻¹•hour⁻¹). During the third hour of testing, numbers of mounts with intromission were similar ($P > 0.10$) among treatments A, B, and C ($0.93, 1.4, \text{ and } 1.7 \pm 0.5$ (\pm SEM) mounts with intromission•bull⁻¹•hour⁻¹, respectively); Treatments A and B were similar ($P > 0.10$) to Treatment D, whereas, mounts with intromission tended ($P = 0.055$) to be higher in Treatment C compared to D. During the final hour of testing, when bulls were in

Treatment A, they exhibited more mounts with intromissions ($P < 0.001$ in all cases) compared to when they were in the other treatments during this time (4.6 versus 2.4, 0.3 and 0 ± 0.7 (\pm SEM) mounts with intromission•bull⁻¹•hour⁻¹, respectively). Furthermore, when bulls were in Treatment B they exhibited more mounts with intromissions compared to when they were in either Treatments C or D during this time (2.4 versus 0.3 and 0 mounts with intromission•bull⁻¹•hour⁻¹, $P < 0.01$ in both cases). Mounts with intromission were similar ($P > 0.10$) during the fourth hour when bulls were in either Treatments C or D, respectively.

Tests for linear, quadratic, and cubic, effects of time within each treatment suggested the following. Mounts with intromission in Treatments A and B changed across time in a cubic fashion ($P < 0.004$ and $P < 0.02$, respectively) whereas they decreased in a quadratic manner ($P < 0.03$) when bulls were in Treatment C. Obviously, no regression could be fit within Treatment D.

Aborted Mounts

Treatments tended to influence the expression of aborted mounts ($P = 0.057$). Least square mean aborted mounts (\pm SEM) for Treatments A, B, C, and D were 2.6, 2, 2.9, and 1.3 ± 0.47 (\pm SEM) aborted mounts•bull⁻¹•hour⁻¹, respectively). Aborted mounts were similar ($P > 0.10$) when bulls were in Treatments A, B, and C. There were more aborted mounts expressed when bulls were in either Treatment A or C compared to when bulls were in Treatment D ($P < 0.05$ and $P < 0.05$, respectively); aborted mounts averaged across all four hours were similar ($P > 0.10$) when bulls were in Treatments B versus D.

The fixed effect of time was significant ($P < 0.0001$) in the analysis of variance for aborted mounts. Averaging across all treatments, days and replicates, aborted mounts decreased in a quadratic fashion ($P < 0.0001$). Least square means (\pm SEM) for aborted mounts during Hours 1, 2, 3, and 4 were 3.8 ± 0.4 , 1.9 ± 0.4 , 1.2 ± 0.3 , and 1.9 ± 0.3 aborted mounts•hour⁻¹, respectively. Aborted mounts were higher ($P < 0.02$) during the first hour when compared pairwise to all subsequent hours of testing. In addition, aborted mounts during the second and fourth hour of testing were significantly higher

($P < 0.05$) when compared to aborted mounts during the third hour of testing. Aborted mounts during the second and fourth hour were similar ($P > 0.10$). Aborted mounts changed over time in a quadratic fashion ($P < 0.0001$) when averaged across all treatments.

The treatment by time interaction was significant ($P < 0.0001$) in the analysis of variance for aborted mounts. Figure 9 illustrates this interaction. During the first hour, least square mean aborted mounts were higher ($P < .05$) when bulls were in Treatments B and C (4.9 and 5.5 aborted mounts•bull⁻¹•hour⁻¹, respectively) versus when they were in Treatments A and D (2.3 and 2.4 aborted mounts•bull⁻¹•hour⁻¹, respectively; SEM = ± 0.87). During the second hour, bulls exhibited more aborted mounts when they were in Treatments A (2.9 aborted mounts•bull⁻¹•hour⁻¹) versus Treatments B and D (0.9 and 1.6 aborted mounts•bull⁻¹•hour⁻¹, $P < 0.02$ for both) but similar ($P > 0.10$) to when they were in Treatment C (2.6 aborted mounts•bull⁻¹•hour⁻¹; SEM = ± 0.67). When bulls were in Treatment C they exhibited more aborted mounts (2.6 aborted mounts•bull⁻¹•hour⁻¹) than when they were in Treatment B (0.9 aborted mounts•bull⁻¹•hour⁻¹, $P < 0.05$), and tended ($P = 0.07$) to exhibit more mounts when they were in Treatment D (1.2 aborted mounts•bull⁻¹•hour⁻¹). Aborted mounts were similar ($P > 0.10$) when bulls were in Treatment B versus Treatment D (1.2 versus 0.9 aborted mounts•bull⁻¹•hour⁻¹) during this time. Aborted mounts were similar during the third hour of testing regardless of treatment (1, 1, 2.1, and 1 (SEM = ± 0.6) aborted mounts•bull⁻¹•hour⁻¹, $P > 0.10$). During the fourth hour, aborted mounts were highest when bulls were in Treatment A compared to when they were in other treatments (3.93 versus 1.5, 1.5, and 0.6 ± 0.6 aborted mounts•bull⁻¹•hour⁻¹, $P < 0.05$ in all cases), wherein aborted mounts were similar ($P > 0.10$) during the last hour among Treatments B, C, and D.

Tests for linear, quadratic, and cubic, effects of time within each treatment suggested the following. Aborted mounts change over time in Treatment A in a cubic fashion ($P < 0.03$) whereas aborted mounts most closely fit a decreasing quadratic function over time when bulls were in Treatment B ($P < 0.05$). No regression equation could be fit to the temporal aspects of the data with regard to Treatments C or D.

Mounting Intervals

Mounting intervals were calculated using a computer spreadsheet. The time (hh:mm:ss) for each mounting event (mounts with intromission or aborted mounts) was entered; for each mounting event, a standardized starting time was adopted, which reflected the apex of the bulls' mount (i.e. the point at which the bull was no longer moving in an upward direction). After calculating each mounting interval for every bull x treatment x replicate combination (delineated by hour), the average time interval was calculated within each hour for every male/female pairing. This number was transformed into a fractional number (i.e. a specific fractional point lying on the continuum from 00:00:00 to 24:59:59) and converted to total seconds by multiplying by 86,400. If no mounting took place (i.e. no mount with intromission nor aborted mount), an assumed 3600 second interval was placed in this cell corresponding to the correct hour's observation.

The fixed effects of treatment, time, the treatment by time interaction, and replicate were all significant in the analysis of variance for mounting interval. Other interactions involving replicate were not significant ($P > 0.10$).

The effect of treatment was significant ($P < 0.05$) in that when bulls were in Treatment A, mounting intervals were shorter than when bulls were in Treatment D (1181 seconds•bull⁻¹ versus 2167 seconds•bull⁻¹). Mounting intervals were similar when bulls were in Treatments A, B, or C, respectively (1180, 1658, and 1705 ± 284 seconds•bull⁻¹•treatment⁻¹).

The treatment by time interaction associated with mounting interval is diagrammed in Figure 10. During the first hour mounting intervals were similar ($P > 0.10$ when bulls were in Treatments A, B, C, and D (1330.6, 810.8, 1023.8, 1206.8 ± 414 seconds•bull⁻¹•treatment⁻¹, respectively). During the second hour of testing, mounting intervals were greater ($P < 0.05$) when bulls were in Treatments C and D (2026.4 and 2188.4 seconds•bull⁻¹, respectively) compared to when bulls were in Treatments A and B (735.1 and 1044 seconds•bull⁻¹, respectively). Mounting intervals were similar ($P > 0.10$) when Treatments C and D were compared as were mounting intervals between Treatment A

and B ($P > 0.10$). During the third hour of testing mounting interval was similar when bulls were in Treatments A, C, and D (1827.7, 1763.7, 2126.6 seconds•bull⁻¹); mounting interval during the third hour of behavior testing was longer ($P < 0.05$) when bulls were in Treatment B (3125 seconds•bull⁻¹) compared to when bulls were in Treatments A and C (1827.7 and 1763.7 seconds•bull⁻¹). Mounting intervals were similar when bulls were in Treatment B compared to when they were in Treatment D (3125 and 2126.6 seconds•bull⁻¹, respectively) during this hour of testing. Analysis of mounting intervals during the fourth hour indicated that bulls in Treatment A had shorter mounting intervals (829 seconds•bull⁻¹) compared to when bulls were in either Treatment C or Treatment D (1970.6 and 2653 seconds•bull⁻¹, $P < 0.05$ and $P < 0.01$, respectively) which was similar ($P = 0.13$) to mounting intervals when bulls were in Treatment B during the fourth hour tests (1655 seconds•bull⁻¹). When bulls were in Treatment B, mounting intervals tended to be less (1655 seconds•bull⁻¹, $P = 0.056$) than those compared to when bulls were in Treatment D (2653 seconds•bull⁻¹) and were similar ($P > 0.10$) to when bulls were in Treatment C (1970.6 seconds•bull⁻¹). Mounting intervals during the fourth hour of the behavior tests were similar ($P > 0.10$) when bulls were in Treatments C and D (1970.6 seconds•bull⁻¹ and 2653 seconds•bull⁻¹, respectively).

Tests for linear, quadratic, and cubic, effects of time within each treatment suggested the following. Mounting intervals changed in a cubic manner when bulls were in Treatments A and B ($P < 0.01$ and $P < 0.002$) whereas mounting interval increased in a linear manner when bulls were in Treatment D. No significant regression could be fit to the data associated with when bulls were in Treatment C (linear, $P = 0.26$; quadratic, $P = 0.44$; and cubic, $P = 0.27$).

Replicate was a significant effect ($P < 0.02$) in the analysis of variance in that bulls in Replicate 1 had longer mounting intervals compared to bulls in Replicate 3 (2254 seconds•bull⁻¹ versus 945 seconds•bull⁻¹). Bulls in Replicate 3 tended ($P = 0.09$) to have shorter mounting intervals compared to bulls in Replicate 2 (945 versus 1833.7

seconds•bull⁻¹). Least square mean mounting intervals were similar ($P > 0.10$) between bulls in Replicates 1 and 2 (2254 and 1833.7 seconds•bull⁻¹, respectively).

Flehmen Responses

The analysis of variance for expression of flehmen responses revealed significant effects associated with time, the treatment by time interaction, and replicate. Treatment was not a significant ($P > 0.10$) fixed effect in the analysis. Interactions involving replicate were not significant ($P > 0.10$).

The fixed effect of time was significant ($P < 0.001$) in the analysis of variance and suggested that more flehmen responses were exhibited ($P < 0.01$) during the first hour of testing compared to numbers of flehmen responses during Hours 2, 3, and 4 (2.4 versus 1.07, 0.46, and 0.85 flehmen responses•bull⁻¹, respectively). Numbers of flehmen responses exhibited during Hours 2 and 4 were similar (1.07 and 0.85 flehmen responses•bull⁻¹) which were both greater ($P < 0.05$) than the number of flehmen responses exhibited during the third hour (0.46 flehmen responses•bull⁻¹). The overall temporal changes associated with the time effects on expression of flehmen responses fit a quadratic function most significantly ($P < 0.0001$).

The analysis of variance showed a significant treatment by time interaction ($P < 0.005$) associated with numbers of flehmen responses. This interaction is shown in Figure 11. During the first hour least square mean flehmen responses were similar ($P > 0.10$) when bulls were in Treatments A, C, and D (1.9, 3.2, and 3.1 flehmen responses•bull⁻¹); when bulls were in Treatment B, there was a tendency for exhibition of fewer flehmen responses compared to when bulls were in Treatments C and D (1.3 versus 3.2 and 3.1 flehmen responses•bull⁻¹, $P = 0.07$ and $P = 0.08$, respectively). During the second hour of testing there was a tendency ($P = 0.08$) for exhibition of more flehmen responses when bulls were in Treatment A versus when bulls were in other treatments (1.69 versus 0.8, 0.9, 0.8 flehmen responses•bull⁻¹, respectively). During the third hour of testing, numbers of flehmen responses among treatments was similar (0.3, 0.5, 0.49, and 0.5 flehmen responses•bull⁻¹, for Treatments A, B, C, and D, respectively).

By the fourth hour of testing, when bulls were in Treatment A, there were significantly more flehmen responses compared to when bulls were in Treatment C or D (1.5, versus 0.5 and 0.3 flehmen responses•bull⁻¹, $P < 0.05$). When bulls were in Treatment B, intermediate numbers of Flehmen responses were exhibited, resulting in statistical similarity ($P > 0.10$) to Treatments A, C, and D, respectively (1 versus 1.5, 0.5, and 0.3 flehmen responses•bull⁻¹, comparing Treatment B pairwise).

Tests for linear, quadratic, and cubic, effects of time within each treatment suggested the following. No significant regression equation ($P > 0.10$ for linear, quadratic, and cubic in all cases) could be fit to describe changes in flehmen behavior across time in Treatments A and B, whereas when bulls were in treatment C and D, flehmen responses decreased in a quadratic fashion ($P < 0.005$ in both cases).

The effect of replicate was significant ($P < 0.05$) in the analysis of variance in that bulls in Replicate 3 exhibited more numbers of flehmen responses, on average, than bulls in either Replicate 1 or 2 (1.8 versus 0.95, 0.82 flehmen responses•bull⁻¹ within replicate, respectively). Least square mean flehmen responses were similar between bulls in Replicate 1 when compared to bulls in Replicate 2.

Discussion

By sequentially pairing mature, sexually experienced adult bulls to unrestrained, variable stimulus females, we were able to ascertain temporal and treatment effects that interacted to influence the expression of most bull sexual behaviors studied. Novelty and receptivity of the female incentive stimuli appeared to be the most important variables to consider when evaluating the temporal expression of bull sexual behaviors under these study conditions.

It was obvious that when bulls were exposed to nonreceptive, diestrus females, they were completely disallowed from exhibiting mounts with intromission. This was not at all surprising and, in fact, this treatment was included simply as a negative control. Bulls apparently were motivated to attempt mounting of diestrus females as demonstrated by Figure 9, however, there was a precipitous decrease in the expression

of aborted mounts as subsequent tests ensued. In part, this would disagree with the notion that bulls will not attempt mounting of nonestrous females, wherein, they only sniff their vulvae to determine receptivity (Sambraus, 1971, cited and translated by Blockey, 1976). Under our study conditions (i.e. small pens with a 1:1 male to unrestrained female pairing), when bulls were in Treatment D, they tested the receptivity of females, at least in part, by attempting mounts. As suggested by Sambraus (1971, cited and translated by Blockey, 1976) and Price (1987) it is axiomatic that nonestrous females display aversive behaviors upon attempted mounting by the bull, which in this experiment resulted in all mounting events when bulls were in Treatment D being categorized as aborted mounts.

Interestingly, mounting interval was not different during the first hour when bulls were in Treatment D when compared to the other treatments. Perhaps by pairing bulls with a nonreceptive female during the first hour, bulls repeatedly attempted mounts relatively close in time for most of the first hour but exhibited few aborted mounts during the latter part. Since mounting intervals can not tell us, precisely, when the mounts were occurring relative to the start of the test, this could be speculative. Apparently, bulls exposed to a diestrus female expressed aborted mounts mostly during the first hour test and intermittently attempted mounting throughout subsequent tests resulting in a dramatic linear increase in mounting intervals from Hour 1 through Hour 4. Within Treatment D least square means for Hours 1, 2, 3, and 4 were 1206, 2188, 2621, 2653 seconds•bull⁻¹•hour⁻¹, wherein Hours 2, 3, and 4 are similar ($P > 0.10$) but all different from Hour 1 ($P < 0.05$, respectively; superscripts not shown on Figure 10). What is not speculative, however, is that the temporal effects of pairing bulls with the same diestrus females were associated with decreased expression of aborted mounts; so much so, that no polynomial equation (e.g. linear, quadratic, or cubic) could be fit to this data.

During Hour 1, the expression of total mounts and mounts with intromission were similar when bulls were in Treatments A, B, and C as were the time intervals between mounting events (with or without intromission). This was not surprising as all stimulus

females were assumed to be similar with respect to novelty and receptivity during the first hour. The effect of novelty on the expression of total mounts and mounts with intromission during these experiments seems apparent when looking at the second through the fourth hours. When bulls were paired with a receptive, familiar female during Hour 2 (i.e. Treatment C) there was a significant decrease in total mounts and mounts with intromission compared to when bulls were coupled with novel females (i.e. Treatments A and B). In addition, mounting intervals increased substantially when bulls were paired with either a novel, receptive female (i.e. Treatment A) or a familiar, receptive female (i.e. Treatment B and Treatment C), similar ($P > 0.10$) to mounting intervals when bulls were paired with nonreceptive, diestrus females. It is apparent that unrestrained, receptive females have a threshold for allowing repeated mounts with intromission which has been known for some time. Price (1987) cited unpublished data that suggested receptive females become refractory to copulation after 4-8 complete copulations (i.e. "services"). It is difficult to evaluate this under our study conditions based on the fact that we did not differentiate between bull intromission with or without a deep, final pelvic thrust, which is the final criterion for categorizing such behavior as a "service" (Blockey, 1976a; Chenoweth, 1981; Price, 1987). In addition, female aversive behaviors were not quantified and, thus, we can not report the actual data on the females' allowance of repeated complete copulations during the latter tests when they were in Treatment C. It is very likely there would be a strong inverse relationship between completed copulations and female aversive behaviors. Blockey (1976a) reported that some receptive females will allow as many as 10 complete copulations (i.e. "services") by particular bulls while others only allow one completed copulation. Further studies are needed to clarify the incidence of female aversion and its relationship to repeated copulations by bulls.

With the pairing of novel females to bulls when they were in Treatments A and B, Hour 2 least squares mean total mounts and mounts with intromission were higher ($P < 0.05$) while mounting intervals were lower ($P < 0.05$) than when bulls were in Treatments C or D. Flehmen responses, however, seemed insensitive, or highly

variable, to changes in female stimulus conditions by this time, since when bulls were in Treatment A there were more flehmen responses than when bulls were in Treatment B. This seems perplexing as bulls in these two treatments would have similar female stimulus conditions during this time (i.e. a novel, estrual female). The effects of novelty, up to this point, seem clear, however. When bulls were paired with a novel receptive female, they mounted and intromitted more ($P < 0.05$) and expressed mounting behaviors closer in time (i.e. shorter mounting intervals; $P < 0.05$) compared to bulls paired with familiar females during this time.

During the third hour, total mounts and mounts with intromission decreased substantially in both Treatments A and B and were similar to when the bulls were paired to familiar receptive or nonreceptive females (Treatments C and D, respectively). Flehmen responses, again, were similar ($P > 0.10$) during Hour 3 among all treatments and, thus, insensitive to changes in receptivity and novelty of female stimulus animals. Hence, even though estrual females introduced to bulls in Treatment A were novel, this novelty was not enough to stimulate further mounts with intromission, aborted mounts, nor flehmen responses. Mounting intervals were similar during the third hour when bulls were in Treatments A, C, and D, respectively. Treatment B bulls had longer mounting intervals during the third hour compared to treatments A and C. Upon closer inspection of the data, we can see how time interacts with treatments between Hour 2 and Hour 3 by comparing the change between Hour 2 and Hour 3 within each treatment. With respect to Treatments A and B, there was a significant increase in mounting intervals from Hour 2 to Hour 3 (Hour 2 versus Hour 3, Treatment A, 735 to 1837 seconds•bull⁻¹, $P < 0.03$; Hour 2 versus Hour 3, Treatment B, 1044 vs. 3125 seconds•bull⁻¹•hour⁻¹, $P < 0.0001$). Similar comparisons within Treatments C and D revealed that mounting intervals do not change ($P > 0.10$) between Hours 2 and 3, respectively. Further corroboration of these suggestions is indicated by the tests for linear, quadratic and cubic trends to each treatment. When bulls were in Treatment C, no regression equation could describe that data, whereas, mounting intervals increased in a linear fashion across all hours when bulls were in Treatment D.

We do not know the exact mechanism(s) that caused this decrease in copulation activity during Hour 3 in bulls that were paired with either a novel, estrual female or an alternating familiar, estrual female. It most likely is related to basic, physical fatigue and (or) acute physiological changes that rendered the bulls incapable of further intromission or reduced their motivation to copulate, regardless of the stimulus animal present. Since total mounts and aborted mounts also declined during this time in these treatment groups, decreased mounting activity and copulation after repeated copulatory events are likely important factors governing the expression of sexual behavior in our unrestrained female paradigm. This could have important implications on breeding bulls' capability of detecting and copulating with estrual females in the breeding herd. In addition, the patterns by which bulls and estrual females interact could be important considerations in how bulls distribute copulations among females. Further studies would need to verify the temporal characteristics of copulation patterns in dyadic mating during pasture breeding to further validate the small pen tests we have used herein.

A novel, receptive female in the final hour of testing stimulated bulls to resume mounts with intromission and aborted mounts, and thus total mounts, to a higher degree than when bulls were paired with familiar estrual females. In addition, mounting intervals were significantly lower ($P < 0.05$) during Hour 4 when bulls were introduced to a novel, receptive female compared to the other stimulus female conditions, although, statistically, mounting interval was similar ($P > 0.10$) when bulls were in Treatment A versus Treatment B during the fourth hour. If bulls became sexually satiated during Hour 3, regardless of female stimulus conditions, then this response in Hour 4 could be characterized as the Coolidge effect. Bulls in Treatment A also exhibited more flehmen responses compared to bulls in Treatments C and D, although the incidence of these was similar in number compared to bulls in Treatment B during the final hour. When bulls received alternating exposure to 2 estrual females, there was a trend of stimulation during the final hour in that bulls resumed mounting and intromission to a higher magnitude than when bulls were in Treatment C. When

bulls were in Treatment B, total mounts and mounts with intromission changed in a cubic fashion ($P < 0.02$) whereas mounts with intromission decreased in a quadratic fashion when bulls were in Treatment C. Interestingly, aborted mounts and flehmen responses were similar ($P > 0.10$) during the final hour when bulls were in Treatments B, C, and D. Hence, it is possible, that the males during the fourth hour of testing in Treatments A and B, after a general state of fatigue had subsided, were stimulated by either a novel female or a familiar female, with the difference being more total mounts and mounts with intromissions ($P < 0.05$) in Treatment A and a numerical increase in the frequency of these intromissions, although not statistically different. Hence, resumption of male mounting activity may not solely be a function of novelty of the stimulus animal but also the degree to which mounts with intromission have occurred in the past. To my knowledge, this is the first detailed description of these phenomena in the bovine.

The difference between bulls' responses to familiar females between Treatments B and C during the fourth hour could be related to the degree to which females received intromissions during the second and third hours of behavior testing, respectively. Total mounts, aborted mounts, and mounting intervals were all similar ($P > 0.10$) when bulls were in Treatments B and C during these times. However, when bulls were paired with a familiar, but rested, estrual female (i.e. Treatment B), mounts with intromission were higher during the fourth hour compared to bulls paired with the same estrual female for four hours (i.e. Treatment C). Females paired with males in Treatment B during the fourth hour (which are the same females from Hour 2) would have been allowed some postconsummatory recovery during Hour 3 since they were not with bulls. Females paired with bulls in Treatment C were not allowed such a rest. In spite of the fact that there seem to be a general lack of sexual activity across treatments during Hour 3, when bulls were in Treatment C during this time, mounts with intromission were significantly higher than those in the previous hour within the same treatment ($P < 0.001$). This strongly suggests that females do not totally cease being receptive following several copulations as Chenoweth (1981), Price (1987) and Blockey (1976a)

suggested. Perhaps females merely require more time to recover from repeated copulations before resumption of appetitive behaviors and subsequent copulations. Further studies could be designed to help determine whether introduction of a novel bull would positively stimulate a sexually satiated female to resume copulatory activity. In the paper by Alexander et al. (1984), the introduction of a novel estrual female did increase the mounting activity of cows on certain days of their estrous cycles, however, they concluded that time of exposure was an important mitigating factor. Further research to determine the extent to which the Coolidge effect is a sexually dimorphic phenomenon in the bovine seems warranted based on these observations. To my knowledge, this is the first suggestion of such a possibility.

In summary, this experiment tested the hypothesis that systematically pairing sexually experienced bulls with females of varying receptivity and novelty would effect the expression of sexual behavior in 60-minute, small pen behavior tests. The results obtained from this experiment suggest that female novelty and receptivity each independently affected the overall expression of bull sexual behavior. Female novelty and receptivity also interacted with time such that a period of sexual satiety in the bulls could not be overcome simply by the addition of a novel, receptive female. After a period of sexual inactivity, however, bull sexual behavior became fully restored in terms of total mounting events and frequency of these events. Under our study conditions, bulls displayed flehmen responses in a highly variable manner that seemed independent of female novelty and receptivity. Moreover, our results suggest that females play an important role in modulating the complex, oscillating pattern of dyadic mating in the bovine and, furthermore, do possess some level of sexual libido.

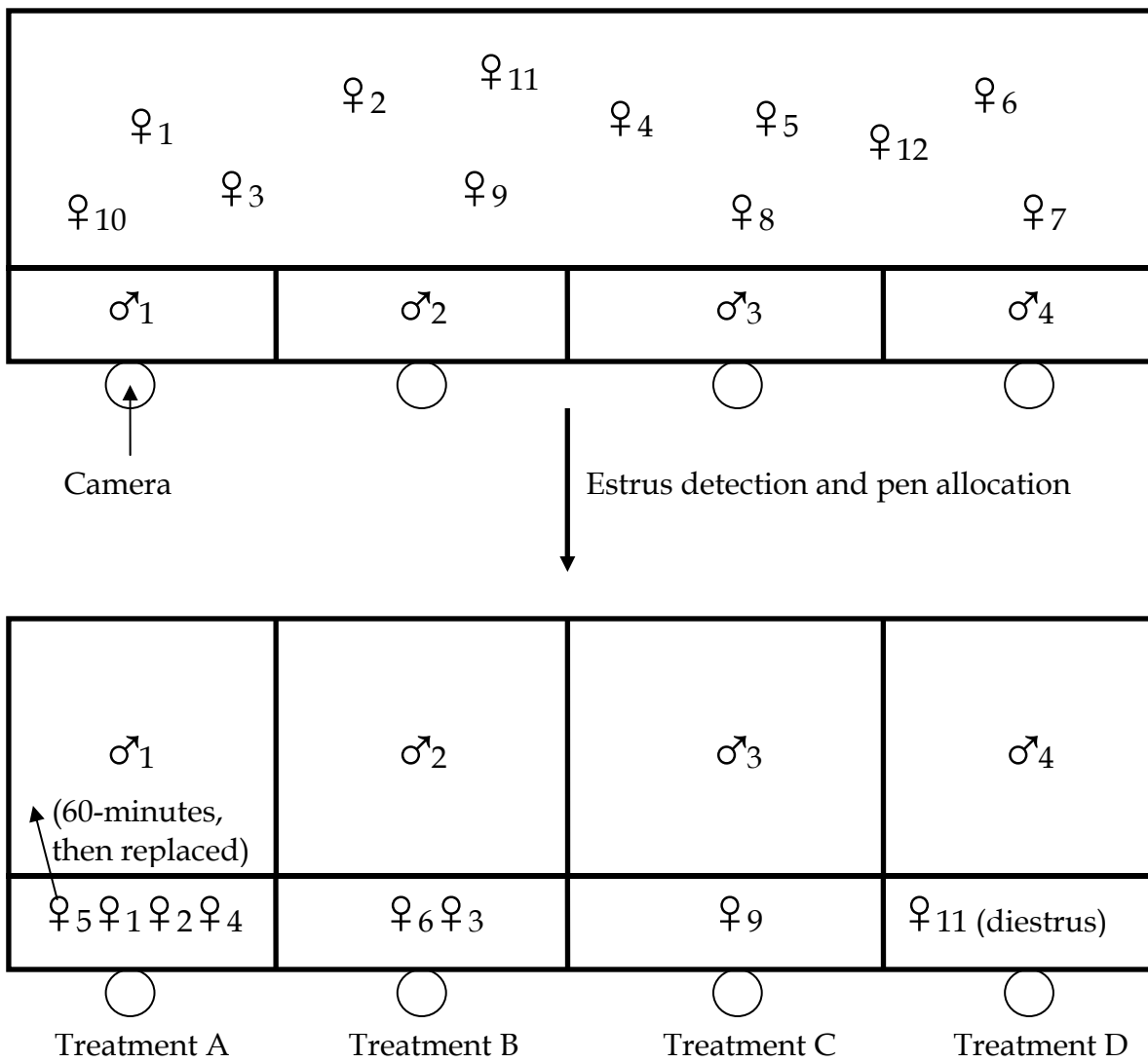


Figure 6. Diagram (not to scale) detailing experimental procedure and apparatus for Experiment 1. On test days, females were allowed to interact in a large observation pen, sequestered from males. After 7 females were determined to be in estrus, experimental animals were allocated to pens according to a Latin square arrangement. Females were paired with males for 60-minutes, then removed, then replaced according to treatment (see text for details) for a total of 4, 60-minute behavior tests. The experiment was replicated 3 times with a total of 12 bulls.

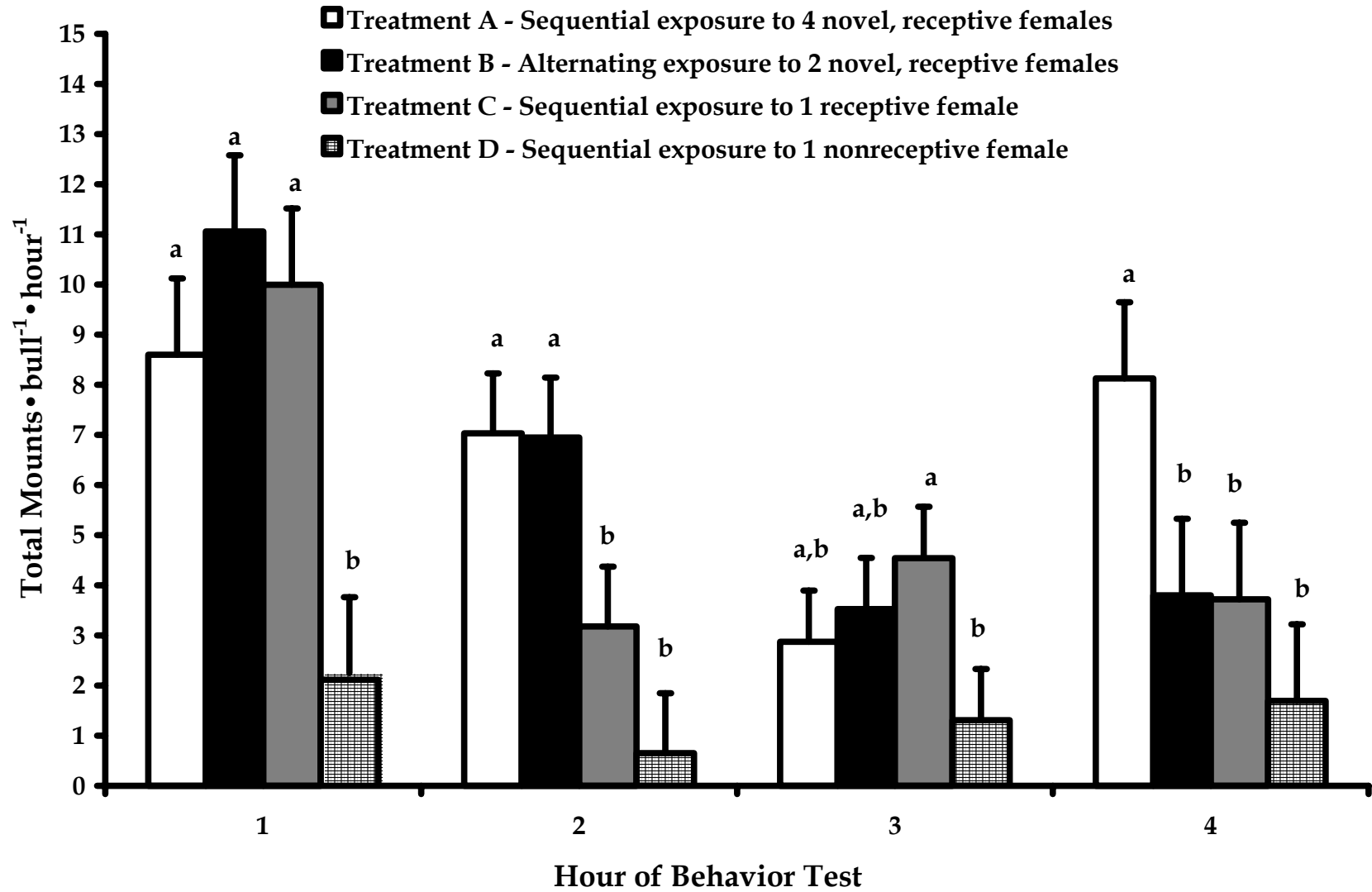


Figure 7. Treatment by time interaction for total mounts. Data presented are least square mean total mounts•bull⁻¹•hour⁻¹ (\pm SEM) when bulls were in Treatments A, B, C, and D for the 4, 60-minute behavior tests. Total mounts changed across time in a cubic manner when bulls were in Treatments A ($P < 0.05$) and C ($P < 0.05$), whereas, total mounts decreased linearly ($P < 0.05$) when bulls were in Treatment B. No regression equation ($P > 0.10$) could be fit to the data when bulls were in Treatment D. Least square means with different superscripts within time differ at $P < 0.05$.

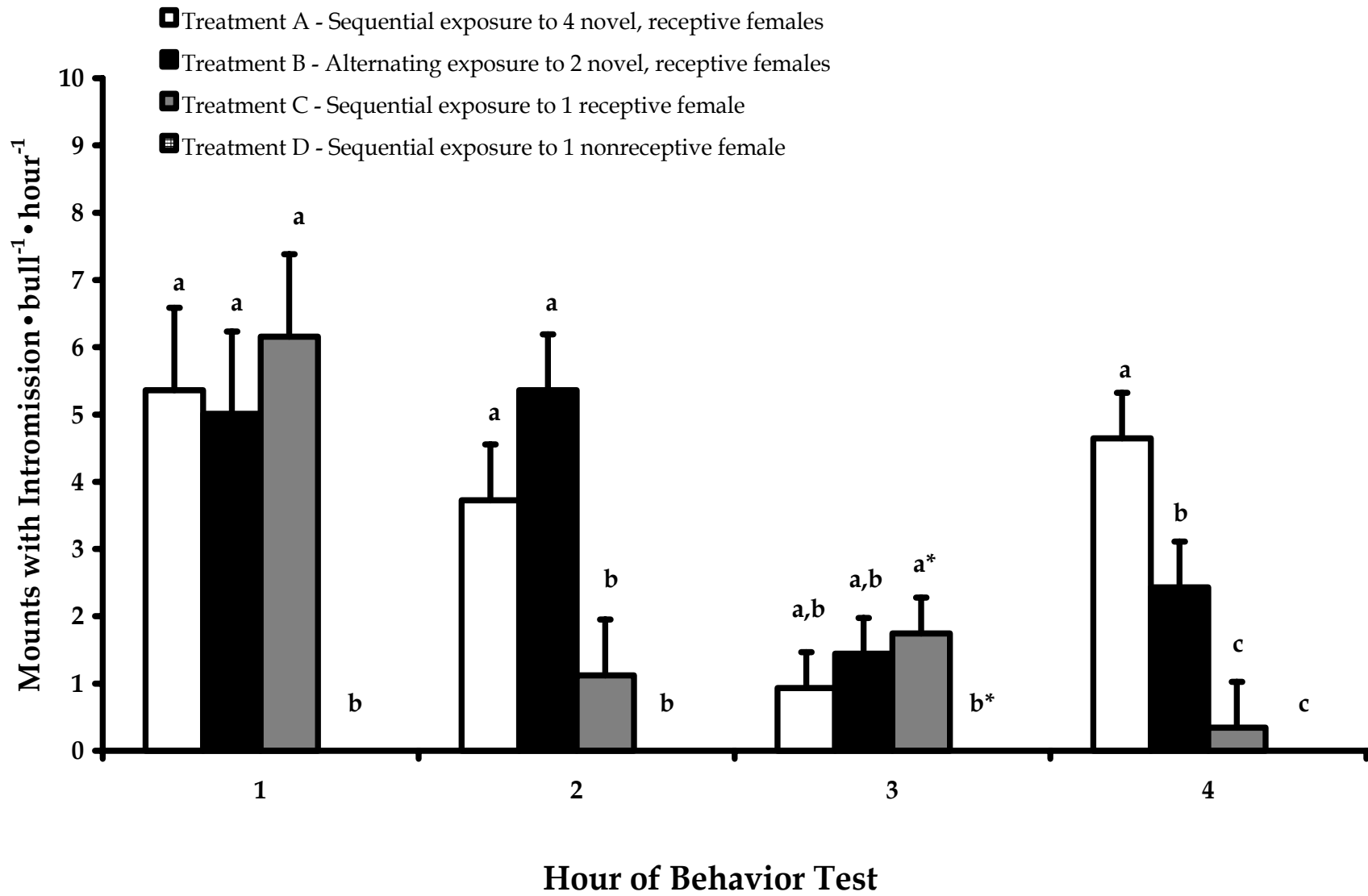


Figure 8. Treatment by time interaction for mounts with intromission. Data presented are least square mean mounts with intromission \bullet bull⁻¹ \bullet hour⁻¹ (\pm SEM) for bulls in Treatment A, B, C, and D for the 4, 60-minute behavior tests. Mounts with intromission in Treatments A and B changed across time in a cubic fashion ($P < 0.004$ and $P < 0.02$, respectively) whereas they decreased in a quadratic manner ($P < 0.03$) when bulls were in Treatment C. Obviously, no regression could be fit within Treatment D. Least square means with a different superscript within time differ at $P < 0.05$ except for Treatment C versus Treatment B, Hour 3 where $P = 0.055$.

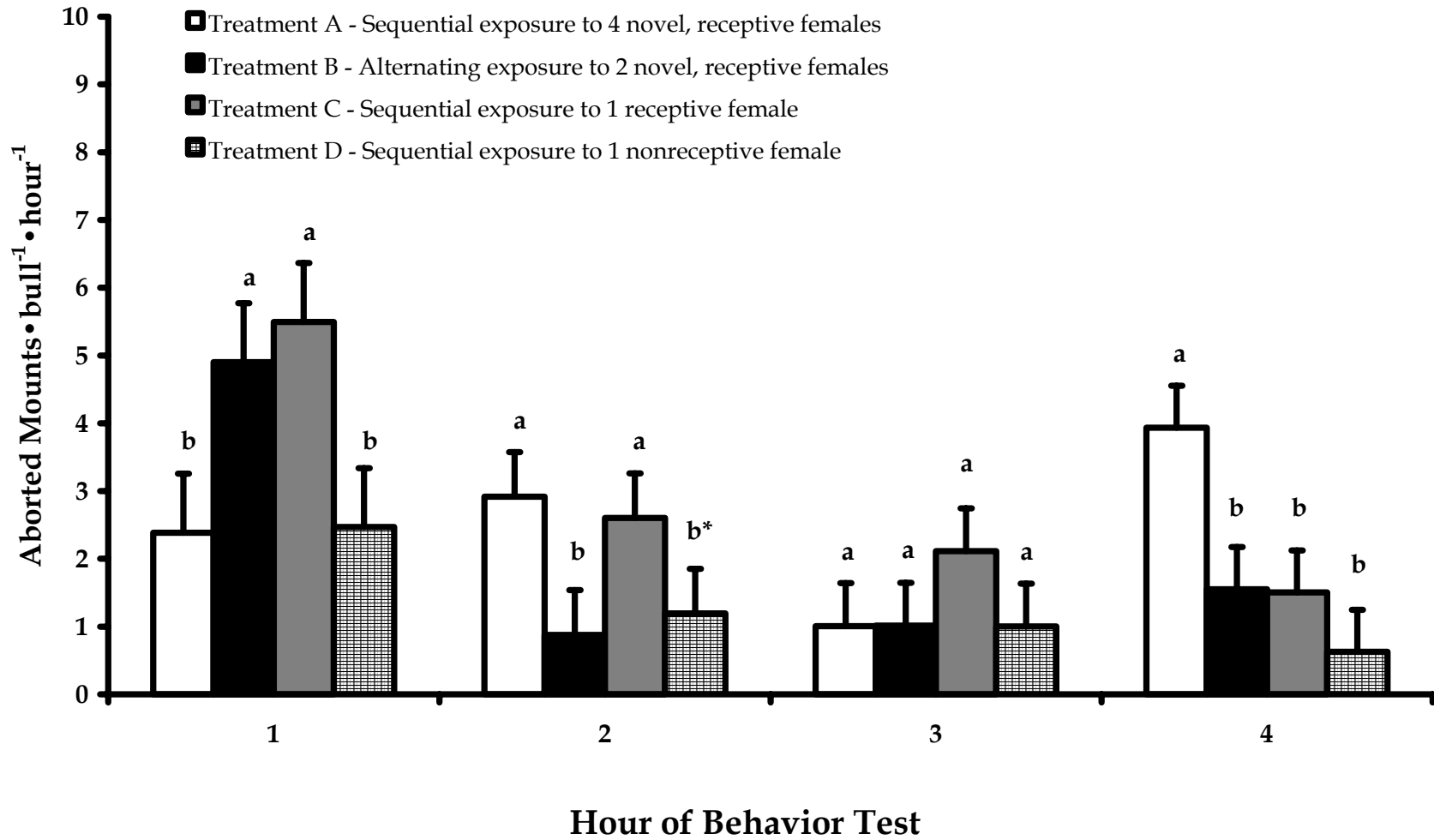


Figure 9. Treatment by time interaction for aborted mounts. Data presented are least square mean aborted mounts•bull⁻¹•hour⁻¹ (± SEM) for bulls in Treatment A, B, C, and D in the 4, 60-minute behavior tests. Aborted mounts change over time in Treatment A in a cubic fashion ($P < 0.03$) whereas aborted mounts most closely fit a decreasing quadratic function over time when bulls were in Treatment B ($P < 0.05$). No regression equation could be fit to the temporal aspects of the data with regard to Treatments C or D. Least square means with a different superscript within time differ at $P < 0.05$ except for Treatment C versus Treatment D, Hour 2, $P = 0.08$.

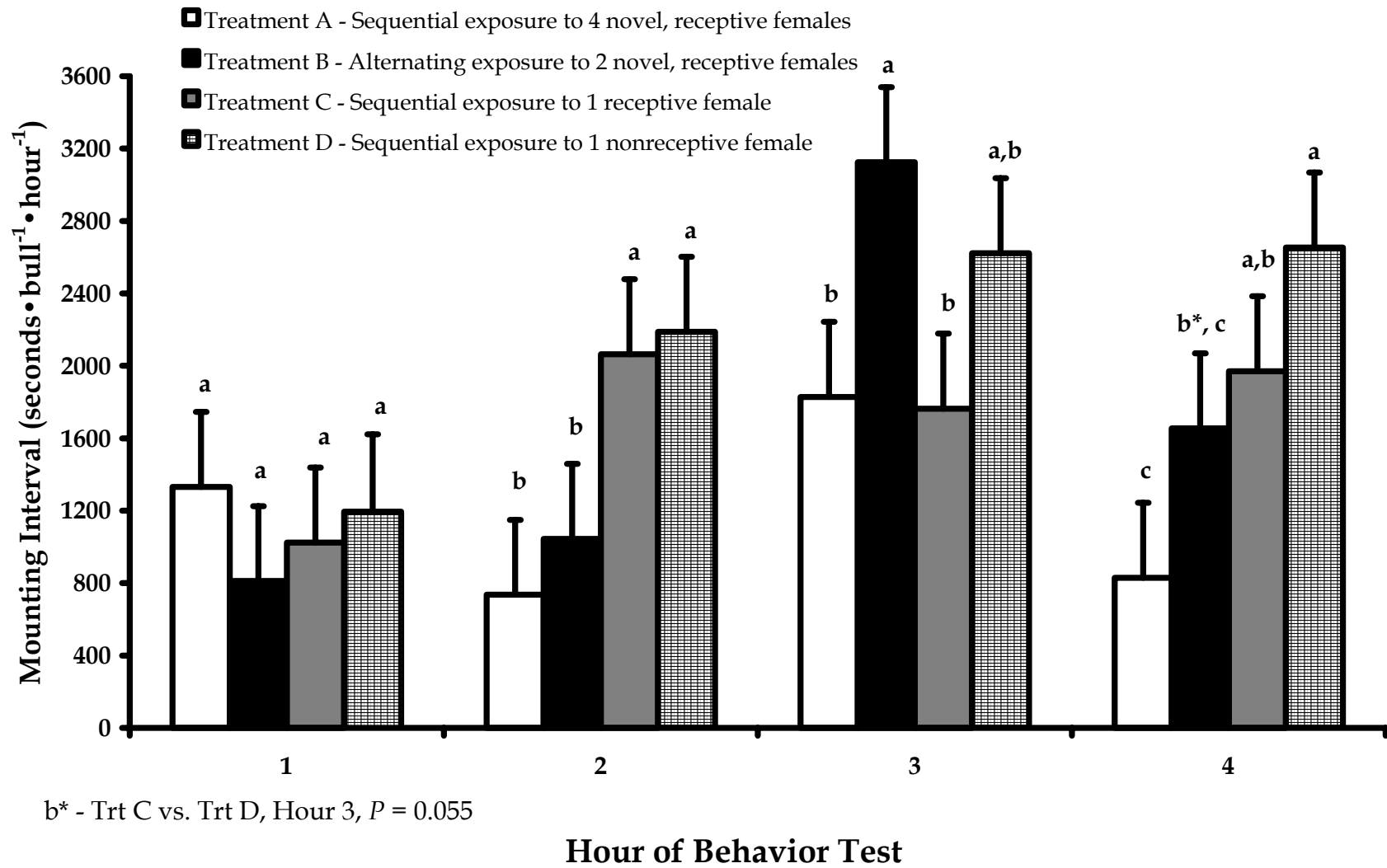


Figure 10. Treatment by time interaction for mounting intervals. Data presented are least square mean mounting intervals in seconds•bull⁻¹•hour⁻¹ (\pm SEM) for bulls in Treatment A, B, C, and D in the 4, 60-minute behavior tests. Mounting intervals changed in a cubic manner when bulls were in Treatments A and B ($P < 0.01$ and $P < 0.002$) whereas mounting intervals increased in a linear manner when bulls were in Treatment D. No significant regression could be fit to the data associated with when bulls were in Treatment C. Least square means with a different superscript within time differ at $P < 0.05$ except for Treatment B vs. Treatment D, Hour 4, $P = 0.056$.

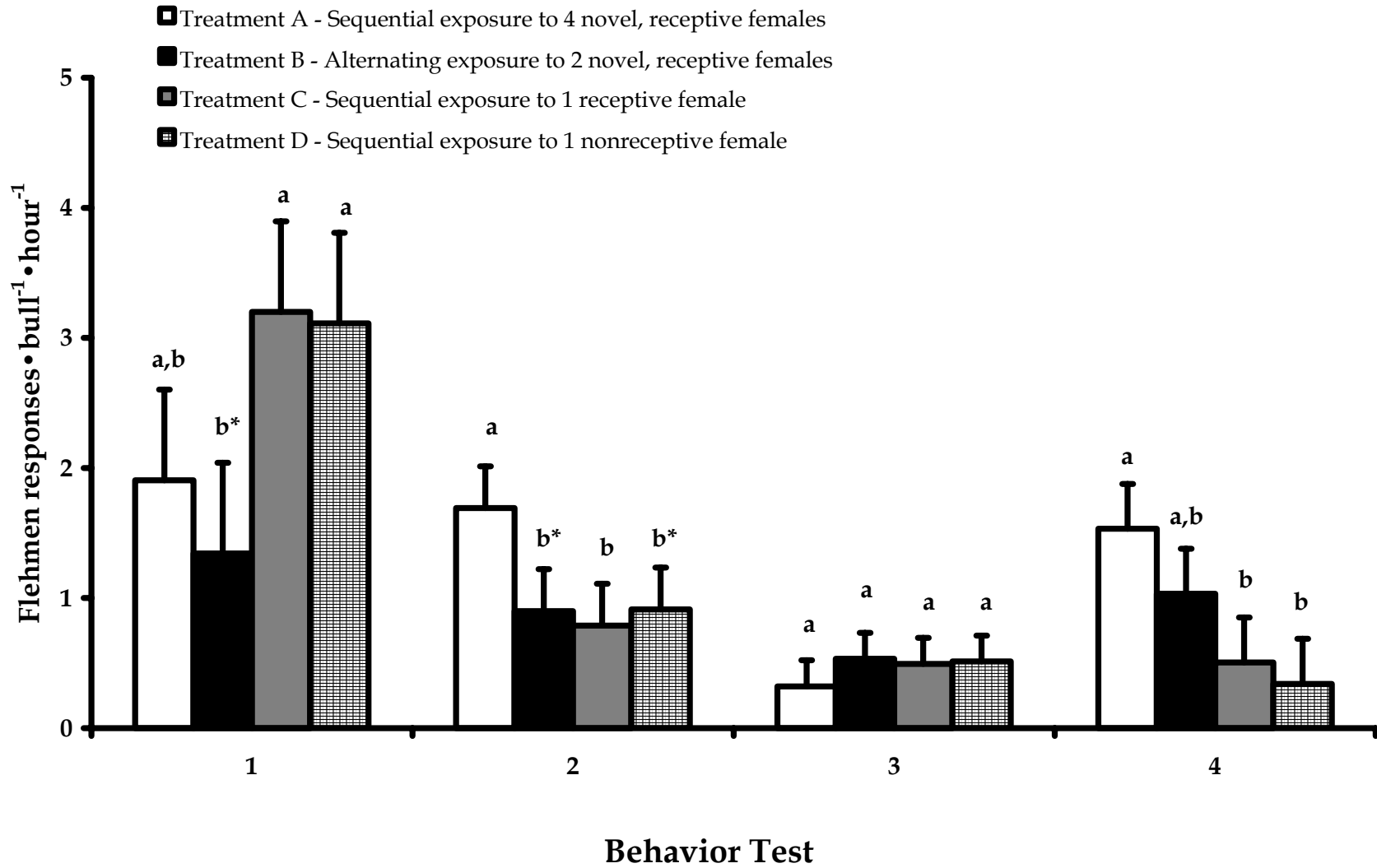


Figure 11. Treatment by time interaction for flehmen responses. Data presented are least square mean flehmen responses •bull⁻¹•hour⁻¹ (\pm SEM) for bulls in Treatment A, B, C, and D in the 4, 60-minute behavior tests. No significant regression equation ($P > 0.10$) could be fit to describe changes in flehmen behavior across time in Treatments A and B, whereas when bulls were in treatment C and D, flehmen responses decreased in a quadratic fashion ($P < 0.005$ in both cases). Least square means with a different superscript within time differ at $P < 0.05$ except for Treatment B vs. Treatments C and D, hour 1, $P = 0.07$ and $P = 0.08$ and Treatment A vs. Treatments B and D, hour 2, $P = 0.08$, respectively.

Chapter Three

Effects of Serial or Group Exposure to Variable Female Stimuli on the Temporal Expression and Repeatability of Sexual Behavior in the Adult Male Bovine

Introduction

In the experiment described in the previous chapter, bulls exposed to novel, estrual females displayed more mounts with intromission more often when compared to bulls exposed to familiar, estrual females. In addition, when bulls were paired with a diestrus female they exhibited fewer sexual behaviors farther apart in time when compared to when bulls were paired with estrual females. Apparently, the motivation of bulls to express these sexual behaviors was affected by both novelty and receptivity of the stimulus females. Temporally, resumption of bull sexual behavior during a third hour of testing with a novel, estrual female was precluded by an unknown mechanism(s). This mechanism was likely related to acute fatigue, sexual satiety, and (or) other physiological changes in these bulls which disrupted their expression of sexual behaviors associated with mounting and intromission. However, the behavioral responses of bulls to novel females during the final hour of testing were appreciable in both magnitude and frequency. In addition, we found that when females were given some period of rest between sexual behavior tests, they, too, showed some renewed interest in copulating. These results cast doubt on the notion that sexual behavior in the bull is expressed in a manner that is independent of the context of the female and merely associated with "innate" libido. However, this very notion is presupposed by researchers employing conventional methods to quantify bull sexual behavior. Conventional methodology advocates sedation and restraint of females in "service stanchions" and the testing of males and females in ratios where the number of males

far exceeds that of females. This conventional approach to studying bull sexual behavior ignores potentially important interactions between unrestrained males and females within dyadic mating contexts in which bovine sexual behavior oscillates. It is also within this interactive context that natural mating occurs and an ethological approach to studying sexual behavior could provide additional information concerning patterns of mating in the natural breeding herd.

One of the most important management decisions beef producers make, which has the potential to directly impact overall reproductive efficiency, is what bull-to-female ratio to use in their natural mating herd. Lower herd fertility may occur when male to female ratios exceed approximately 1:50 (Healy et al., 1993). In this study, estrus synchronization failed to provide any advantage in either pregnancy rates or conception day in a 28-day breeding season with cycling, yearling beef heifers and 2-5 year old bulls at a ratio of 1:50 (Healy et al., 1993). Although estrus synchronization has proven to be a valuable tool for enhancing reproductive efficiency by shortening the breeding and, consequently, the calving seasons, this practice also increases the breeding pressure or mating load that bulls are exposed to. Healy et al. (1993) suggested, some bulls may not be able to effectively impregnate all females when a large number of them are in estrus and receptive simultaneously. There were no attempts in the Healy et al. (1993) study to determine individual differences in sexual behavior of bulls nor were bulls evaluated from a dominance hierarchy perspective. In fact, few, if any, beef producers have an idea of the sexual proficiency of bulls used in natural mating scenarios. The standard recommendation for a bull to female ratio is 1:25 and this is typically adequate in terms of overall calving percentage and, hence, permits the use of bulls with questionable sexual proficiency. Research has shown that this ratio can under-utilize bulls (Rupp et al., 1977; Hawkins et al., 1988a,b). The use of bulls with questionable sexual proficiency could be an especially important factor associated with decreased profitability in situations where the stocking rate is high due to an abundance of high quality native forage or when estrus synchronization is used in a natural mating herd. Fertility and sexual proficiency of bulls could be useful

parameters to assess in order to optimize bull to female ratios (Rupp et al., 1977), however, these are seldom considered by producers when evaluating potential herd bulls. More research is needed to investigate the optimal interactions between maintenance of bull sexual behavior during the breeding season and optimal male to female ratios, especially when estrus synchronization of females is employed.

A novel approach to studying sexual behavior in the bull was outlined in the previous chapter. Briefly, our method advocated studying sexual behavior of the bull in the context of unrestrained, estrual females. We took advantage of the notion that upon pairing of a bull with a novel, estrual female, sexually sated bulls reinitiate the expression of sexual behaviors, specifically, attempted mounting and mounts with intromission (i.e. complete copulations). This phenomenon is known as the Coolidge Effect. In addition, we removed possible observer effects by developing a method for remote surveillance and data recording of heterosexual behavioral interactions. The data record of each bull/female pairing was then quantified in a laboratory scenario.

We observed a decrease in the overall expression of sexual behavior, both in magnitude and frequency, during a third hour of behavior testing. Based on this observation, we hypothesized that by shortening individual behavior pairings to 30-minute bouts, we might observe continuity in expression of sexual behavior by bulls, thus precluding the decrease in copulation activity we noted in the first experiment during a third, 60-minute mating bout (see Chapter 2). In the present experiment, we also tested the hypothesis that sexually mature bulls equally distribute complete copulations among receptive females when exposed to a small group. It has been suggested by several authors that bulls display patterns of sexual behavior when exposed to estrual females in natural mating contexts. Occurrences of bulls displaying preferences for (or “repeat-breeding”, de Araujo et al., 2003) specific females have been reported by researchers studying both *Bos taurus* bulls (Boyd et al., 1989; Godfrey, 1989) and *Bos indicus* bulls (Silva-Mena et al., 2000). However, not all researchers conclude that bulls show tendencies to preferentially copulate with individual females. Blockey (1976b) reported that *Bos taurus* bulls “serviced” females equally when there were an

adequate number of estrous females (>30) available if considerations of dominance among bulls are ignored.

We were also interested in determining the repeatability of sexual behavior expressed by bulls when exposed to females under varying stimulus conditions. Presently, the recommended tests for evaluating sexual behavior (i.e. “serving capacity” tests with restrained and sedated females or short-duration libido index testing) seem moderately to highly repeatable (Lunstra, 1986; Price, 1987; Landaeta-Hernandez et al., 2001). However, this could be due to the fact that libido indices and scoring methods produce results that would be classified as categorical variables (i.e. non-continuous) and, thus, could produce less variable numerical values for calculations. In addition, bulls subjected to “serving capacity” tests are paired with stimulus females that are not allowed to fully express female sexual behaviors, including both aversive and proceptive behaviors. Since females are not allowed the opportunity to freely interact with the bull, they are not allowed to have influence on bull sexual behaviors. This could decrease within bull variance, thus, increasing repeatability estimates. This increase in repeatability might be useful for predictive purposes but could obfuscate underlying biological principals associated with heterosexual mating interactions in a natural mating scenario. As we saw in the first experiment, absence of female receptivity can easily alter the ability of bulls to achieve copulations.

In the previous experiment, females losing receptivity often displayed aversive or avoidance behavior when bulls attempted mounts. Perhaps in a natural mating scenario, this behavior would motivate the bull to find another estrous female. Apparently, some bulls will remain with a nonreceptive female, sniffing perineal and vulvae and attempting to mount while other bulls will immediately move to a different, more receptive female (Blockey, 1976a). Perhaps unrestrained females displaying proceptive behaviors influence bulls’ pattern of sexual behavior. Wohanka (1962; cited by Hurnik, 1987) noted that sexually receptive cows seek proximity to bulls and actively participate in pre-copulatory behaviors, including tactile stimulation through rubbing, nuzzling and (or) licking. These proceptive behaviors, as well as female mounting

activity, may serve to elicit changes in bull sexual behavior. Hence, in this experiment, I subjected a group of bulls (n=12) to two different testing paradigms on eight different occasions to determine if sexual behaviors vary among individuals and whether such behavior was repeatable. The two paradigms I used involved exposing bulls to stimulus females for 2 hours either serially (i.e. one novel, estrual female in 4, 30-minute testing bouts) or to a group of 4 estrual females for an equivalent amount of time (i.e. 2 hours).

Materials and Methods

General

This experiment utilized a simple crossover design with repeated measures. The experiment was conducted between December 12, 2002 and January 3, 2003. Sexual behavior tests were conducted on 8 different occasions during this 22 day period. With the exception of Behavior Test #7, behavior tests were conducted every 4 days. Due to the formation of a thick sheet of ice in the observation pens, Behavior Test #7 was postponed which resulted in an interval of 8 days between Behavior Tests 6 and 7. All procedures were conducted at the University of Kentucky, Animal Research Center in Woodford County, KY. All experimental procedures conducted on animals were approved by the University of Kentucky Institutional Animal Care and Use Committee.

Males

Twelve Black Angus bulls were randomly chosen from a larger contemporary group (n=16) of bulls who had been reared and housed together. Bulls were then randomly assigned to three different bull testing groups (Bull Groups 1, 2, and 3, respectively). The order by which bulls were tested within each of the eight test days was stratified based on these groups. This procedure was followed in order to ensure that the order of testing would not be confounded within bulls. Bulls within bull group were randomly assigned to a particular pen on testing day.

Bulls were born between February 12, 2001 and April 10, 2001. At the beginning of the experiment, the mean (\pm SEM) age of bulls within testing groups was 640, 642, and 633 \pm 8.8 days, respectively. Bull age was similar ($P > 0.10$) among the 3 testing groups.

Mean (\pm pooled SEM) body weights of the bulls within testing groups, measured at the beginning of the experiment, were 658, 607, 637 \pm 20 kg, respectively. Bull body weights were similar ($P > 0.10$) among the 3 bull groups.

All bulls were kept as a group in pastures (6.07 hectares) with *ad libitum* access to water and forage while receiving periodic access to a supplemental protein, energy and trace mineral ration. All bulls received forage based diets plus supplemental feed designed to meet National Research Council requirements for mature bulls (NRC, 1996). During the behavior tests animals did not have access to food or water.

Before conducting this experiment, all bulls had been subjected to a standard breeding soundness exam (Spitzer et al., 1988) performed by a licensed veterinarian. All bulls used in this experiment were deemed acceptable for breeding based on Breeding Soundness Exam criteria.

Females

A large group of intact females was available for use as sexual incentive stimuli. Sixty-seven predominantly Black Angus females were blocked into three herds (Female Groups 1, 2, and 3; n=22, 22, and 23, respectively) based on homology of ovarian structures (i.e. presence of a large *corpus luteum*) and synchrony of estrus following i.m. injection of Lutalyse[®] (Pharmacia & Upjohn, Kalamazoo, MI) followed 24 hours later by an i.m. injection of estradiol cypionate (Pharmacia & Upjohn, Kalamazoo, MI). Females were of various ages ranging from 20 months to 9 years of age; however, the exact dates of birth were unavailable for analysis.

Mean (\pm SEM) body weights of the females in Group 1, 2, and 3 (measured at the beginning of the experiment) were 614.8, 600.6 and 548.7 \pm 18.7 kg, respectively. Females in Group 3 were significantly lighter ($P < 0.01$) at the start of the experiment

than females in Group 1 but were similar ($P > 0.10$) to females in Group 2. Body weights were similar ($P > 0.10$) between females in Groups 1 and 2, respectively.

All females were maintained in groups on pastures (6.07 hectares each) at the University of Kentucky Animal Research Center, Woodford County, Kentucky, with *ad libitum* access to water and forage while receiving periodic access to a supplemental protein, energy and trace mineral ration designed to meet National Research Council requirements for nonlactating, mature beef females (NRC, 1996). During behavior testing, animals did not have access to food or water.

Estrus Induction for Sexual Behavior Tests

Females received an i.m. injection of Lutalyse® 9 to 17 days after the first observed estrus induced during the previous ultrasonography and selection period. Thereafter, each group of females received Lutalyse® 10 days after observed estrus to maintain synchrony of cyclicity. Approximately 24-hours after Lutalyse® injection females were injected i.m. with 0.5 mL (1 mg) of estradiol cypionate to induce behavioral estrus. This induction protocol induced behavioral estrus approximately 16-36 hours after estradiol cypionate administration for approximately 12-16 hours in 90-95% of the females, which is in close agreement with the research of Pancarci et al. (2002). In a large observation pen (29.6 m X 3.7 m), before the sexual behavior tests began, females were visually examined for signs of standing estrus and only heifers in estrus were used as stimulus females. Criteria for estrus included mounting and standing firm to at least 3 mounts, indicated by no lateral or forward movement after being mounted.

Behavior Test Procedure

Bulls were assigned to treatments (n=2) based on a randomly chosen crossover arrangement. Treatments were alternated across the eight behavior test dates within each bull (A then B, or B then A, etc., for each bull) such that half the bulls within each bull group were on the same treatment each testing day. Treatments were, A) sequential exposure to 4 estrual females, one every 30-minutes (A), and 2) exposure to a group of 4 estrual heifers for 2 hours (B). Behavior tests on days 1-8 were conducted

between approximately 1900 h and 0200 h, 1700 h and 2400 h, 1500 h and 2200 h, 1600 h and 2300 h, 1300 h and 2000 h, 1600 h and 2300 h, 1400 h and 2100 h, and 1300 h and 2000 h, respectively. Ambient air temperatures on testing days, during these specific times, ranged from -0.6°C to 3.3°C , -8°C to -5°C , 0°C to 2.2°C , 0.5°C to 2.8°C , 11.7°C to 13.3°C , 0.5°C to 6°C , 11.7°C to 13.3°C , and -2.2°C to -1.7°C , respectively.

The order of bull group testing was stratified across the 8 testing days (e.g. Day 1 order of testing - 1, 2, 3; Day 2 order of testing - 2, 3, 1, etc.). The same group of females receiving estrus induction treatment served as stimuli animals for all 3 groups of bulls on each particular test day. Since estrus in the bovine lasts approximately 15 hours and the total time to test all three groups of bulls was approximately 6 hours, I made the assumption that females would allow repeated copulations by more than one male during the 6 hours of testing. On occasions where females became nonreceptive to mounting and intromission by bulls, or where other animal welfare concerns arose, I removed them from the test pen and immediately replaced them with a new, estrual female.

As in the previous experiment, all bulls were given the opportunity to become pre-stimulated by visually observing homosexual mounting activity of the females occupying the large observation pen on each test day. The group of bulls being tested first on a particular test day occupied small, adjacent pens ($7.4\text{ m} \times 1.85\text{ m}$) during its pre-test stimulation period. Bulls being tested second and last on a particular day were placed in their respective groups in one of two larger adjacent pens ($7.4\text{ m} \times 3.7\text{ m}$). Hence, these bulls received additional opportunity for visual stimulation by observing heterosexual mating. The flooring in the observation pen and large adjacent pens were fine gravel whereas the flooring in the small adjacent pens which housed testing bulls individually was concrete.

When the necessary number ($n=16$) of estrual females were determined to be in standing estrus, females were removed from the large observation pen and placed in an adjacent holding pen, still separated from the bulls. Gates within the large observation pen were then closed and firmly latched, resulting in 4 testing pens of equal size (7.4 m

X 3.7 m). Bulls were then allowed into testing pens wherein the bulls' ID numbers and pen locations were recorded and cross referenced to the randomized treatment arrangement. Estrual stimulus females were then randomly allocated within the pretest observation pens (i.e. 4 estrual females per pen). At this point all animal ID numbers were meticulously recorded and cross referenced. Once the arrangement was verified, the video equipment was set to record all events in all pens simultaneously on one video cassette tape, and the test was begun. Bulls were exposed to estrual females either serially (i.e. 1:1 male-to-female ratio, switched every 30-minutes; Treatment A) or as a group (i.e. 1:4 male-to-female ratio for 2 hours; Treatment B). After the first group of bulls was tested, females were then re-randomized by commingling them into a large group followed by randomly separating them into the small adjacent pens in groups of 4 females•pen⁻¹. The second group of bulls to be tested was then separated into the observation pens and subsequent tests could begin. The last group of bulls was tested in a similar manner. Figure 12 diagrams the experimental design for one testing day. Sexual behavior of bulls was recorded and quantified using the techniques outlined in the previous chapter.

Statistical Analyses

The design of this experiment was a simple crossover with repeated measures. Dependent variables were numbers of total mounts, mounts with intromissions, aborted mounts, mean mounting interval, and numbers of flehmen responses, all taken from both the 4, 30-minute behavior tests and the 2-hour behavior tests within Treatments A and B, respectively. Temporal data within the 2-hour tests (i.e. Treatment B) were delineated at 30-minute intervals to provide comparative data at these time points.

These data were subjected to analysis of variance using the PROC MIXED procedure of the Statistical Analysis System (SAS, v. 8.02, Institute, Cary, IN). The models contained fixed effects for treatment, time (i.e. 30-minute bouts nested within test day), test day, order of testing, and bull group, in addition to the interactions of treatment x time, treatment x order, treatment x bull group, bull group x time, bull group x

treatment, test day x time, and treatment x time x bull group. Data were modeled using animal within treatment as random subject effects and bull group was used as a random group effect; both effects were included in the model to account for possible between subject heterogeneity (Littell et al., 2000). Using the techniques of Wolfinger (1996), a first order autoregressive, heterogeneous covariance structure was selected to account for the within-animal correlations for all longitudinal data associated with our dependent variables, except for mean mounting interval where a compound symmetrical covariance structure fit best. Least square means procedures were used to calculate means and standard errors in addition to statistically comparing (pairwise) all significant fixed effects and their interactions. In addition, an analysis was performed fitting the treatment regressions on a set of orthogonal polynomials in time up to degree three (thus, a complete set of contrasts for the differences among the four levels of time), and their interactions with the stimulus female treatments. Contrast statements were then included to request tests of linear, quadratic, and cubic, effects of time within each treatment.

In order to evaluate the degree to which bulls distribute mounts with intromission with stimulus females, an additional analysis of variance was conducted using PROC MIXED (SAS, v. 8.02, Institute, Cary, IN). In this analysis, the order in which females received mounts with intromissions, the average number of females receiving mounts with intromission, and the mean mounts with intromission per female delineated by the 30-minute testing bouts were dependent variables. The same process for analyses was described in the preceding section.

I was also interested in calculating repeatability of bulls' sexual behavior. This would give some indication as to how much was gained by the repetition of these measurements and could also be used in developing a prediction equation that could provide information on the potential sexual proficiency of bulls subjected to such tests. I utilized the methods of Falconer and Mackay (1996) wherein they suggested the variance of sexual behaviors (e.g. mounts with intromission) can be analyzed into components within individual bulls, that is, measuring the differences between

performances if the same bull across the eight different days, and a component between individuals, that is, measuring permanent differences between individual bulls in the experiment. The within-bull component is entirely environmental, caused by temporary differences in environment between successive tests (Falconer and Mackay, 1996). The between-bull component is partly environmental and partly genetic, with the environmental portion being caused by circumstances that do not affect the individuals permanently (Falconer and Mackay, 1996). Using the methods of Falconer and Mackay (1996), repeatability was calculated by utilizing the intraclass correlation, $r = \sigma^2_b / (\sigma^2_b + \sigma^2_w)$, where σ^2_b is the variance component between bulls and σ^2_w is the variance component within bulls. The expected mean square within bulls is σ^2_w , whereas, the expected mean square between bulls is composed of $\sigma^2_w + 8 \sigma^2_b$. The coefficient of 8 is used in this case because each bull has 8 different records of sexual behavior data encompassing all test days (Falconer and Mackay, 1996). A similar methodology was employed by Landaeta-Hernandez et al. (2001) to evaluate repeatability of sexual behavior using restrained females in young *Bos taurus* bulls.

One bull (ID # L117) in Bull Group 1 displayed a condition best described as macrophallus. Upon attempts by him to insert his penis into the vagina of a female, the penis would become lodged between the two animals, resulting in a high rate of intromission failure. Hence, it could not be reliably determined to what extent the bull was displaying mounts with intromission versus aborted mounts. In addition, this condition resulted in the bull displaying exceedingly low mounting intervals (approximately 1 mounting event every 25 seconds). I chose to eliminate this bull from all statistical analyses.

Results

Total Mounts

The analysis of variance for total mounts (i.e. mounts with intromission plus aborted mounts) indicated that treatment, time, treatment x time interaction, and test day were all significant ($P < 0.01$).

When bulls were in Treatment A, they exhibited fewer total mounts ($P < 0.0001$) than when they were in Treatment B (Least Square Mean \pm SEM for Treatment A and Treatment B were 5.3 versus 6.8 ± 0.4 total mounts•bull⁻¹•treatment⁻¹, respectively).

Least square mean total mounts decreased over the 4, 30-minute periods in a quadratic fashion. Least square mean total mounts (\pm SEM) for the 4, 30-minute testing bouts were 9.1 ± 0.4 , 6.3 ± 0.5 , 4.6 ± 0.46 , and 4.3 ± 0.4 total mounts•bull⁻¹•30-minute period⁻¹, respectively. Least square mean total mounts were greater for the 1st 30-minute period than for all subsequent 30-minute testing periods; similarly, least square mean total mounts for the 2nd 30-minute test period were greater than least square mean total mounts during the 3rd and 4th, 30-minute testing period, respectively. Least square mean total mounts were similar during the 3rd, 30-minute testing period when compared to those during the 4th, 30-minute testing period.

The treatment by time interaction for total mounts is shown in Figure 13. During the 1st 30-minutes, there were fewer ($P < 0.0001$) least square mean (\pm SEM) total mounts when bulls were in Treatments A versus when they were in Treatment B (6.99 versus 11.2 ± 0.57 , total mounts•bull⁻¹•30-minutes⁻¹). During the 2nd, 3rd, and 4th, 30-minute tests, least square mean (\pm SEM) total mounts were similar ($P > 0.10$) when bulls were in Treatment A versus Treatment B (5.6 versus 6.9 ± 0.63 , 4.3 versus 4.8 ± 0.57 , and 4.2 versus 4.4 ± 0.49 total mounts•bull⁻¹•30-minutes⁻¹, respectively).

Tests for linear, quadratic, and cubic, effects of time within each treatment suggested that least square mean total mounts in Treatment A decreased linearly ($P < 0.001$) across the 4, 30-minute behavior bouts. When bulls were exposed to a group of 4 estrual females for 2 hours (i.e. Treatment B), total mounts decreased in a quadratic manner ($P = 0.0004$).

The effect of test day was significant in the analysis of variance for total mounts. Least square mean (\pm SEM) total mounts for test days 1 through 8 were 6.6, 7.1, 5.4, 6.9, 6.4, 5.7, 5.9, and 4.7 ± 0.59 total mounts•bull⁻¹•day⁻¹, respectively. More total mounts ($P < 0.05$) were expressed on the 2nd day of behavior testing when compared pairwise to behavior testing days 3, 6, 7, and 8, respectively. Total mounts were similar ($P > 0.10$)

among testing days 1, 2, 4, and 5, respectively. Least square total mounts were also similar ($P > 0.10$) among testing days 6, 7, and 8, respectively; they were also similar ($P > 0.10$) among testing days 1, 3, 5, 6 and 7. However, more ($P < 0.05$) total mounts were expressed during testing day 4 when compared pairwise to testing days 3 ($P > 0.05$), 6 ($P = 0.08$), 7 ($P = 0.056$), and 8 ($P < 0.01$), respectively. In addition, there were more total mounts expressed during testing days 1, 2, 4 and 5 versus testing day 8, respectively.

Mounts with Intromission

The analysis of variance for mounts with intromission revealed significant treatment, time, test day, order of testing, and treatment by time interaction effects. All other effects and interactions were not significant ($P > 0.10$) in the analysis.

As one might expect, when bulls were sequentially exposed to receptive females across 4, 30-minute behavior tests, (Treatments A) they exhibited fewer ($P = 0.0001$) mounts with intromission than when exposed to a group of four estrual females for 2 hours (Treatment B) (2.9 versus 4.1 ± 0.25 mounts with intromission•bull⁻¹•treatment⁻¹; Least square mean \pm SEM).

The fixed effect of time was significant ($P < 0.0001$) with respect to mounts with intromission. Averaging across all treatments, testing days and testing orders, mounts with intromission decreased in a quadratic fashion ($P = 0.0003$) across the 2 hours. Least square means (\pm SEM within time) for mounts with intromission for 30-minute behavior tests 1, 2, 3, and 4 were 5.2 ± 0.3 , 3.6 ± 0.3 , 2.6 ± 0.29 , and 2.7 ± 0.27 mounts with intromission•30-minutes⁻¹, respectively. Mounts with intromission were higher ($P < 0.0001$) during the first 30-minute test when compared pairwise to all subsequent 30-minute tests. In addition, mounts with intromission during the second 30-minutes of testing were significantly higher ($P < 0.01$) than mounts with intromission during the third ($P < 0.05$) and fourth ($P < 0.02$) 30-minutes of testing, respectively. Mounts with intromission were similar ($P > 0.10$) between tests 3 and 4, when compared pairwise. The overall temporal change for mounts with intromission across time was best described as a decreasing quadratic function ($P = 0.0003$).

The treatment by time interaction for mounts with intromission is shown in Figure 14. During the first 30-minutes, there were fewer ($P < 0.0001$) mounts with intromission when bulls were in Treatments A versus when in Treatment B (3.1 versus 7.4 ± 0.4 (Least Square Mean \pm SEM) mounts with intromission \bullet bull⁻¹ \bullet 30-minutes⁻¹). During the second, third, and fourth 30-minute tests, least square mean (\pm SEM) mounts with intromission were similar ($P > 0.10$) when bulls were in Treatment A versus Treatment B (3.2 versus 3.9 ± 0.44 , 2.6 versus 2.6 ± 0.37 , 2.9 versus 2.6 ± 0.36 mounts with intromission \bullet bull⁻¹ \bullet 30-minutes⁻¹, respectively).

Tests for linear, quadratic, and cubic, effects of time within each treatment suggested the following. Mounts with intromission in Treatments A did not change across time, as no significant ($P > 0.10$) regression equation could be fit. When bulls were exposed to a group of 4 estrual females for 2 hours (i.e. Treatment B), mounts with intromission decreased in a quadratic manner ($P = 0.0004$).

The analysis of variance revealed a significant order of testing effect ($P < 0.10$). When bulls were tested with females first on a particular testing day, they were allowed to express more mounts with intromission than when tested second or last during the testing day (4.1 versus 3.0 and 3.5 ± 0.3 mounts with intromission \bullet bull⁻¹ \bullet bull group⁻¹, respectively). Mounts with intromission were similar ($P > 0.10$) when bulls were tested either second or last during behavior test days.

The effect of test day was a significant source of variation in the analysis of variance ($P < 0.0001$) for mounts with intromission. Least square (\pm pooled SEM) mounts with intromission for testing days 1 through 8 were 3.7, 4.3, 3.5, 5.3, 3.8, 2.7, 2.6 and 2.3 ± 0.43 mounts with intromission \bullet bull⁻¹ \bullet day⁻¹, respectively. More mounts with intromission were expressed on the fourth day of behavior testing when compared pairwise to all other days ($P < 0.08$). Mounts with intromission were similar ($P > 0.10$) among testing days 1, 2, 3, and 5, respectively. Least square mounts with intromission were also similar ($P > 0.10$) among testing days 6, 7, and 8, respectively; they were also similar ($P > 0.10$) among testing days 1, 3, 5, 6 and 7. However, more ($P < 0.05$) mounts with intromission were expressed during testing day 2 when compared pairwise to testing

days 6, 7, and 8, respectively. In addition, there were more mounts with intromission expressed during testing days 1 and 3 versus testing day 8, respectively.

Aborted Mounts

Neither treatments nor the treatment x time interaction were significant sources of variation in the analysis of variance for aborted mounts ($P < 0.10$). Least square mean aborted mounts (\pm SEM) for Treatments A and B were 2.3 and 2.4 ± 0.24 aborted mounts•bull⁻¹•treatment⁻¹, respectively. Least square mean (\pm SEM) aborted mounts for 30-minute tests 1, 2, 3, and 4 when bulls were in Treatment A versus Treatment B were 3.89 ± 0.4 versus 3.6 ± 0.4 , 2.4 ± 0.4 versus 2.7 ± 0.26 , 1.6 ± 0.3 versus 1.87 ± 0.3 , and 1.47 ± 0.27 versus 1.46 ± 0.27 , respectively. Although not significant, the treatment x time interaction for aborted mounts is shown in Figure 15.

Aborted mounts changed significantly across the 4, 30-minute testing bouts ($P < 0.0001$). Averaging across treatments, testing days and bull groups, aborted mounts decreased in a quadratic fashion ($P < 0.01$). Least square mean (\pm SEM) aborted mounts during 30-minute behavior bouts 1, 2, 3, and 4 were 3.7 ± 0.3 , 2.6 ± 0.3 , 1.7 ± 0.2 , and 1.4 ± 0.2 aborted mounts•30-minutes⁻¹, respectively. Aborted mounts were higher ($P < 0.02$) during the first 30-minutes of testing when compared pairwise to all subsequent 30-minute behavior testing periods. In addition, aborted mounts during the second 30-minute period were significantly higher ($P < 0.05$) when compared pairwise to aborted mounts during the third and fourth 30-minute tests, respectively. Least square aborted mounts during the third and fourth 30-minute tests were similar ($P > 0.10$).

The order in which bulls were tested with stimulus females was significant ($P < 0.01$) in the analysis of variance for aborted mounts. Least square mean (\pm SEM) aborted mounts for bulls tested first, second, and last were 1.9 ± 0.2 , 2.5 ± 0.2 , and 2.7 ± 0.2 aborted mounts•bull group⁻¹, respectively. When bulls were in the first group tested with females on a particular test day, they exhibited fewer ($P < 0.002$) aborted mounts than when they were tested second or last on the testing day, respectively. Least square aborted mounts were similar ($P > 0.10$) when bulls were tested second or last during the test day.

Mounting Interval

Mounting intervals were calculated using the same methodology as in Chapter 2. The fixed effects of treatment, time, and the treatment x time interaction were all significant ($P < 0.05$) in the analysis of variance for mounting interval. Other effects and interactions were not significant ($P > 0.10$).

The effect of treatment was significant ($P < 0.05$) in that when bulls were in Treatment A, least square (\pm SEM) mounting intervals were longer than when bulls were in Treatment B (576 seconds•bull⁻¹ versus 378 \pm 49 seconds•bull⁻¹•30-minutes⁻¹, respectively).

The overall effect of time was significant in that least square mean mounting intervals, when averaged across treatments, increased in a quadratic manner ($P < 0.05$).

The treatment by time interaction associated with mounting interval is diagrammed in Figure 16. During the first 30-minutes of sexual behavior testing, least square (\pm SEM) mounting intervals were longer ($P < 0.05$) when bulls were in Treatments A versus when bulls were in Treatment B (401 versus 165 \pm 85 seconds•bull⁻¹•30-minutes⁻¹, respectively). Similarly, during the second 30-minutes of testing, least square (\pm SEM) mounting intervals were greater ($P < 0.001$) when bulls were in Treatments A versus when they were in Treatment B (699 versus 242 \pm 85 seconds•bull⁻¹•30-minutes⁻¹, respectively). During both subsequent 30-minute bouts (i.e. tests 3 and 4, respectively), least square mean (\pm SEM) mounting intervals were similar ($P > 0.10$) between Treatments A and B (30-minute test 3, 692 versus 539 \pm 85 seconds•bull⁻¹•30-minutes⁻¹; 30-minute test 4, 511 versus 618 \pm 85 seconds•bull⁻¹•30-minutes⁻¹, respectively).

Requests for linear, quadratic, and cubic, effects of time within each treatment suggested that least square mean mounting intervals increased in a quadratic manner when bulls were in Treatments A ($P = 0.07$) whereas mounting interval increased in a linear manner ($P = 0.06$) when bulls were in Treatment B.

Flehmen Responses

The analysis of variance for expression of flehmen responses revealed that the fixed effect of time was significant ($P < 0.0001$) in the analysis of variance. Treatment and the treatment x time interaction were not significant ($P > 0.10$) fixed effects in the analysis. However, there was a significant ($P < 0.001$) treatment x test day interaction (data not shown). All other effects and interactions were not significant ($P > 0.10$).

Least square (\pm SEM) flehmen responses for 30-minute tests 1, 2, 3, and 4 were 3.99 ± 0.38 , 1.9 ± 0.28 , 1.7 ± 0.28 , and 1.4 ± 0.26 flehmen responses•bull⁻¹•30-minutes⁻¹, respectively. More flehmen responses were exhibited ($P < 0.01$) during the first 30-minutes of testing compared to flehmen responses during 30-minute tests 2, 3, and 4, respectively. Numbers of flehmen responses exhibited during 30-minute test 2 and 3 were similar ($P > 0.10$); however, there were significantly fewer flehmen responses during the last 30-minutes of testing compared to the second 30-minutes of testing. Least square flehmen responses were similar ($P > 0.10$) between 30-minute tests 3 and 4, respectively. Hence, the overall temporal change of flehmen responses fit a cubic function most significantly ($P < 0.001$).

Order of Stimulus Females Receiving Mounts with Intromission

The order in which females allowed mounts with intromission to occur was determined by evaluating the mounts with intromission received by each female delineated by the order in which they received them (i.e. first, second, third or fourth). This analysis was conducted to elucidate possible patterns of mating when bulls were exposed to 4, estrual females. The analysis of variance revealed the fixed effects of treatment, female order and the female order x treatment interaction were all significant ($P < .05$, respectively). In addition, the effect of test day was also significant ($P < 0.05$, data not shown). All other effects and interactions were not significant ($P > 0.10$).

The effect of treatment was significant ($P < 0.05$) in that when bulls were in Treatment A least square mean (\pm SEM) mounts with intromission•female⁻¹•treatment⁻¹ were lower ($P < 0.05$) than when bulls were in Treatment B (3.19 versus 4.49 ± 0.33 mounts with intromission•female⁻¹•treatment⁻¹, respectively).

The overall effect of the order in which females allowed mounts with intromission was significant ($P < 0.05$) in that least square mounts with intromission (\pm SEM) were higher ($P < 0.05$) for the first, second, and third females encountered when compared pairwise to the last females allowing mounts with intromission (4.7, 4.4, 3.9 versus 2.3 ± 0.4 mounts with intromission•female⁻¹, respectively).

The treatment by female order interaction ($P < 0.05$) is shown in Figure 17. When bulls were in Treatment A least square mean mounts with intromission•female⁻¹•treatment⁻¹ (\pm SEM) were similar among the first, second, third, and fourth females allowing intromission (3.2, 3.3, 3.04 and 3.2 ± 0.57 for the first, second, third and fourth female allowing mounts with intromission, respectively). When bulls were in Treatment B, least square mounts with intromission•female⁻¹•treatment⁻¹ (\pm SEM) were similar ($P > 0.10$) among the first, second, and third females allowing mounts with intromission but were all higher than the fourth female allowing mounts with intromission (6.1, 5.5, and 4.8 versus 1.4 ± 0.57 , respectively). Additionally, more ($P < 0.05$) mounts with intromission were allowed by the first, second, and third females encountered when bulls were in Treatment B versus when bulls were in Treatment A; however, the fourth females copulating with bulls received more mounts with intromission ($P < 0.05$) when bulls were in Treatment A compared to when they were in Treatment B.

Temporal Distribution of Mounts with Intromission among Stimulus Females

The analysis of variance for average number of females receiving mounts with intromission, independent of the order in which they received them, revealed significant ($P < 0.05$) treatment, time and treatment by time interaction effects. In addition, the order in which bulls were tested and test day were significant ($P < 0.05$) sources of variation (data not shown).

Least square mean (\pm SEM) females receiving mounts with intromission were higher ($P < 0.05$) when bulls were in Treatment A versus Treatment B (0.8 versus 1.92 ± 0.07 females receiving mounts with intromission•bull⁻¹•treatment⁻¹, respectively). In

addition, least square mean (\pm SEM) females receiving mounts with intromission changed over time in a quadratic fashion ($P < 0.02$) and were 1.47, 1.09, 1, and 1.1 ± 0.08 females receiving mounts with intromission•bull⁻¹•30-minutes⁻¹ for 30-minute test bouts 1, 2, 3, and 4, respectively.

The treatment by time interaction for the average number of females receiving mounts with intromission is shown in Figure 18. The treatment by time interaction was significant ($P < 0.0001$) in that when bulls were in Treatment A, least square mean (\pm SEM) females receiving mounts with intromission did not change across 30-minute behavior bouts 1, 2, 3, and 4, respectively, and were 0.85, 0.8, 0.7, and 0.9 ± 0.1 females receiving mounts with intromission•bull⁻¹•30-minutes⁻¹. Least square mean (\pm SEM) females receiving mounts with intromission when bulls were in Treatment B decreased in a quadratic manner ($P < 0.001$) and were 2.7, 2.1, 1.5 and 1.3 ± 0.1 females receiving mounts with intromission•bull⁻¹•30-minutes⁻¹ for 30-minute behavior test bouts 1, 2, 3, and 4, respectively. As one might expect, during the first, second, third and fourth 30-minute behavior test bouts, more ($P < 0.05$, in all cases) females received mounts with intromission when bulls were in Treatment B when compared to when bulls were in Treatment A.

Mounts with Intromission per Female Exposed

Mounts with intromission per female exposed was determined in order to ascertain the average mounts with intromission allowed by each female within the treatments. In the analysis of variance for mounts with intromission per female exposed to the bulls, treatment, time and the treatment by time interaction were all significant ($P < 0.05$). In addition, testing day and the order in which bulls received access to stimulus females were significant ($P < 0.05$, data not shown); other effects and interactions were not significant ($P > 0.10$).

Least square mean (\pm SEM) mounts with intromission per female exposed were higher ($P < 0.05$) when bulls were in Treatment A versus Treatment B (3.1 versus 2.1 ± 0.2 mounts with intromission•female exposed⁻¹•treatment⁻¹, respectively). In addition, least square mean (\pm SEM) mounts with intromission per female exposed tended to

changed over time in a quadratic fashion ($P = 0.07$) and were $3.1, 2.6, 2.2,$ and 2.4 ± 0.27 mounts with intromission•female exposed⁻¹•30-minutes⁻¹ for 30-minute test bouts 1, 2, 3, and 4, respectively.

The treatment by time interaction for the number of mounts with intromission per female exposed is shown in Figure 19. This interaction was significant ($P < 0.05$) in that when bulls were in Treatment A, least square mean (\pm SEM) mounts with intromission per female exposed did not change across 30-minute behavior bouts 1, 2, 3, and 4, respectively, and were $3.2, 3.2, 2.6,$ and 3.2 ± 0.3 females receiving mounts with intromission•female exposed⁻¹•30-minutes⁻¹. Least square mean (\pm SEM) mounts with intromission per female exposed when bulls were in Treatment B decreased in a quadratic manner ($P < 0.01$) and were $3, 2, 1.7$ and 1.6 ± 0.3 mounts with intromission•female exposed⁻¹•30-minutes⁻¹ for 30-minute behavior test bouts 1, 2, 3, and 4, respectively. During the first 30-minutes of sexual behavior testing, mounts with intromission per female exposed were similar ($P > 0.10$) when bulls were in either Treatment A or Treatment B. During the second, third and fourth 30-minute behavior test bouts, more ($P < 0.05$, in all cases) mounts with intromission per female exposed occurred when bulls were in Treatment A versus when they were in Treatment B.

Repeatability of Bull Sexual Behaviors

The repeatability of mounts with intromission and total mounts, overall was low for these variables ($R = 0.12$ for mounts with intromission and $R = 0.15$ for total mounts). The repeatability of ratio of mounts with intromission to total mounts (i.e. success ratio) was somewhat higher at $R = 0.196$ but is still considered low.

Discussion

When allowed to freely interact with 4 unrestrained, estrual females for 2 hours, sexually experienced bulls demonstrated a pattern of sexual motivation consistent with most models of sexual behavior (Pierce et al., 1988; Pfaus, 1996; Agmo, 1999). Namely, several attempted mounts and complete copulations with usually 2-3 of the 4 females for approximately one full hour (i.e. 2, 30-minute bouts) followed by a general decrease

in copulatory activity, as indicated by a marked decrease in total mounting activity, mounts with intromission, the number of females receiving mounts with intromission, numbers of mounts with intromission per stimulus female exposed, and, finally, a lengthening of mounting intervals. On the other hand, bulls sequentially paired with a single, novel, estrual female every 30 minutes for 2 hours did not show the same mating patterns in most of the sexual behaviors quantified. With the exception of total mounts, when bulls were in Treatment A, they did not show a marked decrease in copulatory activity, specifically, mounts with intromission across the 4, 30-minute behavior bouts. Although aborted mounts decreased in both treatments in a quadratic manner, the ratio of successful mounts with intromission to total mounts (i.e. success ratio) increased when bulls were sequentially paired with 4, estrual females (Treatment A, data not shown). Surprisingly, this suggests that as the 2-hour test neared completion, bulls in Treatment A became somewhat more efficient in distributing mounts with intromission across the remainder of novel, unrestrained females during the remaining 30-minute behavior bouts. When bulls were sequentially paired with 4 novel, unrestrained, estrual females the interval between mounting behaviors did increase by the 2nd 30-minute behavior bout but remained stable thereafter. This contrasts with the linear increase in mounting intervals when bulls were in Treatment B.

This increase in mounting interval is not attributable to a decrease in the rate of unsuccessful attempts to gain intromission. Rather, it appears to be related to a decrease in the expression of overall mounts with intromission. When bulls were exposed to a group of estrual females, there were more copulatory behaviors occurring predominantly within the first 30-minutes followed by a declining trend thereafter. However, the ratio of mounts with intromission to total mounts remained stable throughout the remaining 30-minute behavior bouts (data not shown). As previously stated, latter 30-minute bouts were marked by a decrease in the total number of mounts with intromission, the number of females receiving mounts with intromission, and the number of mounts with intromission per stimulus female exposed, resulting in an overall increase in mounting intervals.

The order in which bulls encountered females who allowed mounts with intromission was also an important factor that modulated mounting activity in the bull. Apparently, bulls distributed copulations among 3 of the females (i.e. copulated repeatedly) but did not equally copulate with the fourth female encountered. Perhaps in the context of an estrual group, females elicit repeated copulatory responses from bulls in a manner that interacts with the male's physiological status that precludes his ability to distribute complete copulations equally among receptive females, at least for a period of time. This would mean as bulls becomes fatigued or, possibly, sexually sated, females can no longer elicit the same level of copulatory behavior, both in terms of magnitude and frequency. This contrasts with the work of Blockey (1976b) who reported that *Bos taurus* bulls "serviced" females equally when there were an adequate number of estrous females (>30) available if considerations of dominance among bulls were ignored. Alternatively, under our study conditions, perhaps given additional time with the stimulus females bulls may have recovered and further copulated with the last female in the series, resulting in equal distribution of copulations among the receptive females. Alternatively, after a period of rest, perhaps bulls would have displayed preferential copulations with those females who allowed them most readily.

These findings do extend those reported by researchers studying both *Bos taurus* bulls (Boyd et al., 1989; Godfrey, 1989; de Araujo et al., 2003) and *Bos indicus* bulls (Silva-Mena et al., 2000) who all reported occurrences of bulls displaying preferences for (i.e. "repeat-breeding") specific females. To date, there has not been a detailed study providing an assessment of male copulatory efficiency and variable mating patterns during prolonged male-female interactions. Thus far, conventional methodology (e.g. "serving capacity" and libido index tests with restrained females) provides incomplete information regarding heterosexual copulatory behavior and no information at all about oscillating intromission frequency, which are the critical measures for assessing male reproductive capacity.

Indeed, further research is needed on ascertaining sexual satiety in the bulls during heterosexual mating. By establishing such a criterion, utilizing consistent stopping

point across sexual behavior tests could provide appropriate testing durations and the flexibility necessary for the requirements of particular research questions. Hence, the optimal point to terminate observations seems particularly important. Under our study conditions, perhaps bulls and females would have shown some resumption of mating activity after a period of rest. Apparently, the time required to resume sexual activity varies with the species and behaviors being studied and a satiety criterion could be used to accommodate consideration of these factors (Beach and Jordan, 1956; Beach and Rabedau, 1959; Dewsbury, 1982).

Based on the decline in copulatory behavior and increasing mounting intervals during latter 30-minute testing bouts when bulls were in Treatment B, the possibility that female bovine pace heterosexual mating is evident. Indeed, this phenomenon has been noted in several species. For example, when mounting stimulation is accompanied by intromission and(or) ejaculation during prolonged sexual behavior tests, the probability and intensity of subsequent lordosis is reduced while female aversive behaviors increases (Bermant and Westbrook, 1966; Hardy and Debold, 1972). These aversive behaviors greatly diminish when females are able to pace sexual contact (Pierce and Nutall, 1961; Bermant and Westbrook, 1966; Parades and Alonso, 1997). To my knowledge, there has never been a study conducted on determining the extent to which female aversive behavior, in the context of a small, sexually active group of females, influence bulls' copulatory efficiency. Data from Katz and Price (1986) suggested that bulls that can not intromit and ejaculate (via penile neurectomy and (or) penile deviation) have higher mounting frequencies; the same effect was noted with control bulls (intact penile enervation and placement) paired with females who had patches placed over their vulvae. Katz and Price (1986) further suggested that unrestrained females displayed intermittent periods of unwillingness to stand for mounting, despite their estrual state. Based on these observations, it is possible that intromission and (or) ejaculation by the male induces sexual refractoriness in females.

Although the present results suggests that bulls do not have the capacity to deliver copulations equally to a small group of receptive females, it can be argued that these

results underestimate a bull's capacity for complete copulations if bulls do not repeat breed receptive females. If bulls display full copulations to satiety only in a situation with multiple females (either simultaneously or sequentially) then bulls would be expected to show a Coolidge effect, that is, a reliable resumption of copulation when a novel female is introduced to a satiated male. Under these study conditions, when bulls were sequentially exposed to novel, estrual females for 30-minutes, behavioral patterns perhaps related to the Coolidge effect resulted in a maintenance of mounts with intromission across time and across stimulus females and stability in mounting intervals which suggests that the males in the present study, in fact, had not delivered their full capacity of mounts with intromission. Alternatively, estrual females may have the capacity to pace mounts with intromission, such that sexual satiety in the male was never fully reached in the 30-minute testing bouts, which allowed him to respond to further solicitations from other, novel, and receptive females.

Some authors have reported moderate repeatability of behavior tests with both *Bos taurus* bulls (Chenoweth, 1979; Lunstra et al., 1979 and Lunstra, 1984; Landaeta-Hernandez, 2001). Under our study conditions, repeatability was low and would indicate large environmental influences that could possibly lead to difficulties in interpretation of sexual behavior data (Chenoweth, 1994). Other studies found both moderate ($R=0.44$) and high ($R=0.84$) repeatability when libido was assessed in *Bos indicus* bulls (Pichardo et al., 1982, cited by Landaeta-Hernandez et al., 2001; Piccinalli, 1992). As Price (1987) suggested, such differences between estimates may be due to a number of factors including genes, age and experience, and a lack of a standardized test for bulls. In addition, the use of sexually related behavioral patterns to accurately estimate libido may pose limitations (Price, 1987). Alternatively, based upon the fact that most researchers utilize restrained females and libido indices or other categorical data, variation within bulls could be artificially reduced while not being representative of behaviors expressed under natural mating conditions. Perhaps further studies could determine the repeatability of behaviors when bulls are exposed to natural mating stimuli.

Copulation in the bovine involves active participation by both the male and the female. That a group of heterosexual partners showed a gradual decrease in copulatory activity is consistent with other research on sexual behavior in rodents (Beach and Jordan, 1956; Lorrain et al., 1999; Arteaga et al., 2000) although the time course to recovery of sexual satiety could be quite different between bovine and murine species. The results of the present study suggest that the approach to satiety in the bovine is characterized by increased mounting intervals and by fewer numbers of total mounts and mounts with intromission. Similar changes have been observed in other species, including deer mice (Dewsbury, 1982), rats (Karen & Barfield, 1975), and voles (Gray and Dewsbury, 1973). Since most research studying the male bovine have utilized questionable methods for studying bull sexual behavior, the consistent and progressive increase in mounting intervals with continued 30-minute bouts has not been reported. In general, this characteristic of copulatory behavior has been seen in most rodents (Gray and Dewsbury, 1973). With respect to the sexually experienced, adult male bovine, the satiety process was evident by the gradual but inevitable slowing of sexual activity over time, eventually resulting in little sexual behavior.

Bull Group	1				2				3			
Bull #	1	2	3	4	5	6	7	8	9	10	11	12
Treatment	A	B	A	B	A	B	A	B	A	B	A	B
Females	16 Estrual Females (randomized)				16 Estrual Females (re-randomized)				16 Estrual Females (re-randomized)			

Figure 12. Diagram illustrating the experimental design for Experiment 2. This diagram illustrates one hypothetical test day. Four bulls were tested for 2 hours, according to appropriate treatment (i.e. sequential exposure versus group exposure to 4 estrual females) in 1 of 4 pens (see Figure 6). After the first group of bulls was tested, females were re-randomized and then the second group of bulls was tested and so on for a total of 6 hours of behavior testing. Females displaying aversive behavior during testing were removed and replaced with females in standing estrus. Treatments were assigned to bulls randomly with a simple crossover arrangement and the order in which bull groups were tested was stratified across the 8 different behavior test days.

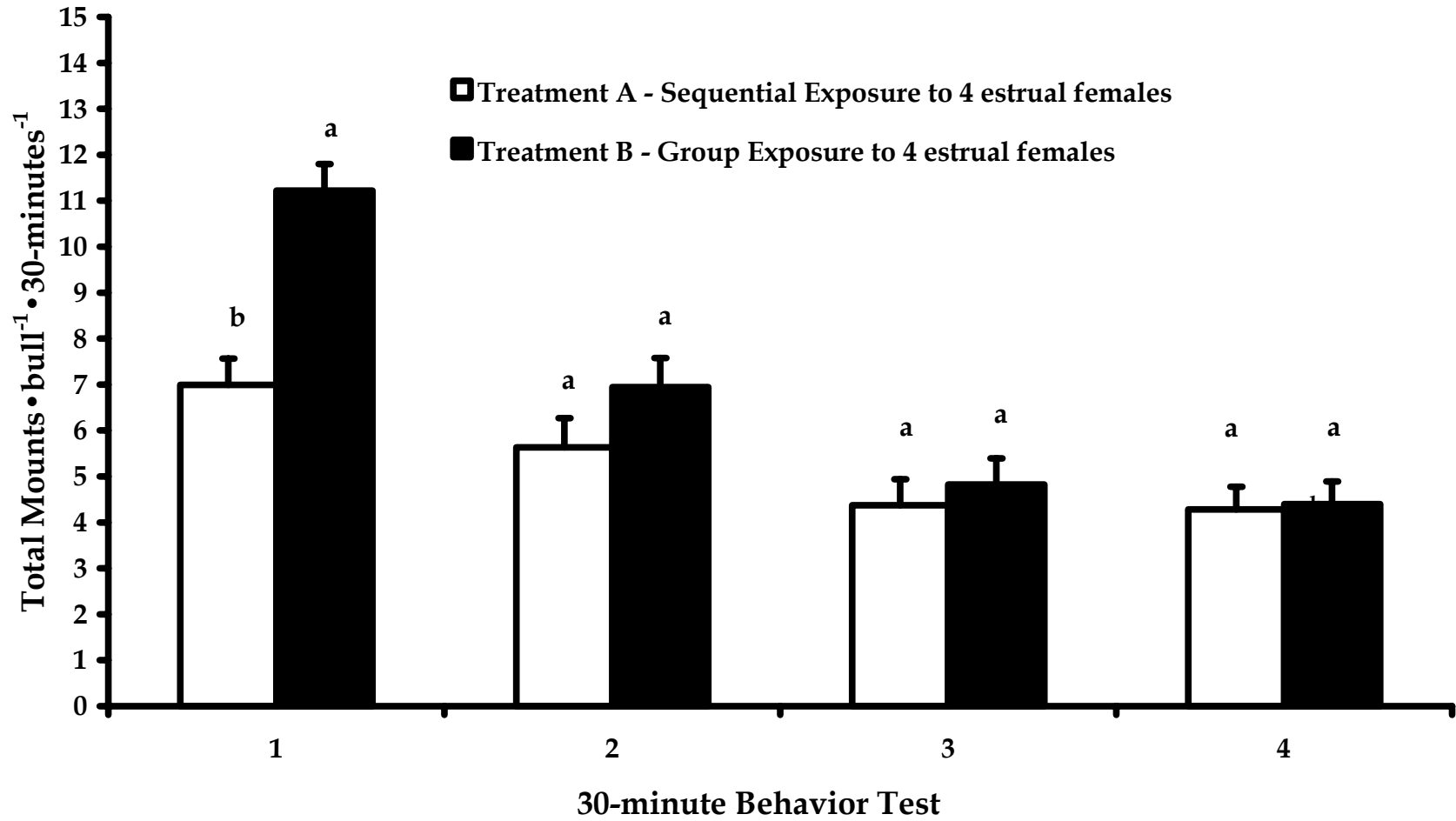


Figure 13. Treatment by time interaction for total mounts. Data presented are least square mean total mounts•bull⁻¹•30-minutes⁻¹ (\pm SEM) when bulls were in Treatment A and B for the 4, 30-minute behavior bouts. Total mounts in Treatment A decreased linearly ($P < 0.001$) across the 4, 30-minute behavior bouts, whereas, when bulls were exposed to a group of 4 estrual females for 2 hours (i.e. Treatment B), total mounts decreased in a quadratic manner ($P = 0.0004$). Least square means with a different superscript within time differ at $P < 0.05$.

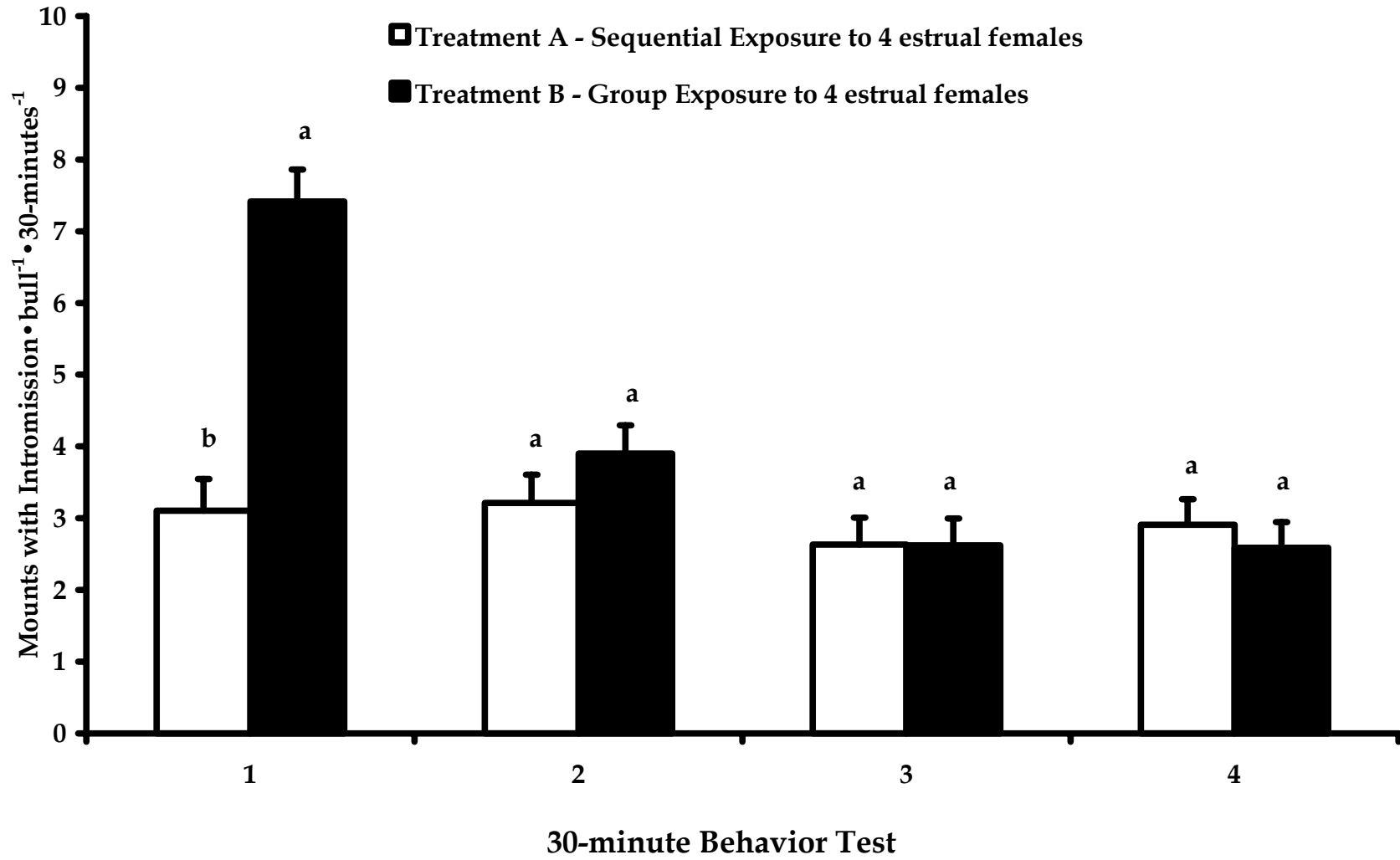


Figure 14. Treatment by time interaction for mounts with intromission. Data presented are least square mean mounts with intromission \bullet bull⁻¹ \bullet 30-minutes⁻¹ (\pm SEM) when bulls were in Treatments A and B for the 4, 30-minute behavior bouts. Mounts with intromission in Treatments A did not change across time, as no significant ($P > 0.10$) regression equation could be fit. When bulls were exposed to a group of 4 estrual females for 2 hours (i.e. Treatment B), mounts with intromission decreased in a quadratic manner ($P = 0.0004$). Least square means with a different superscript within time differ at $P < 0.05$.

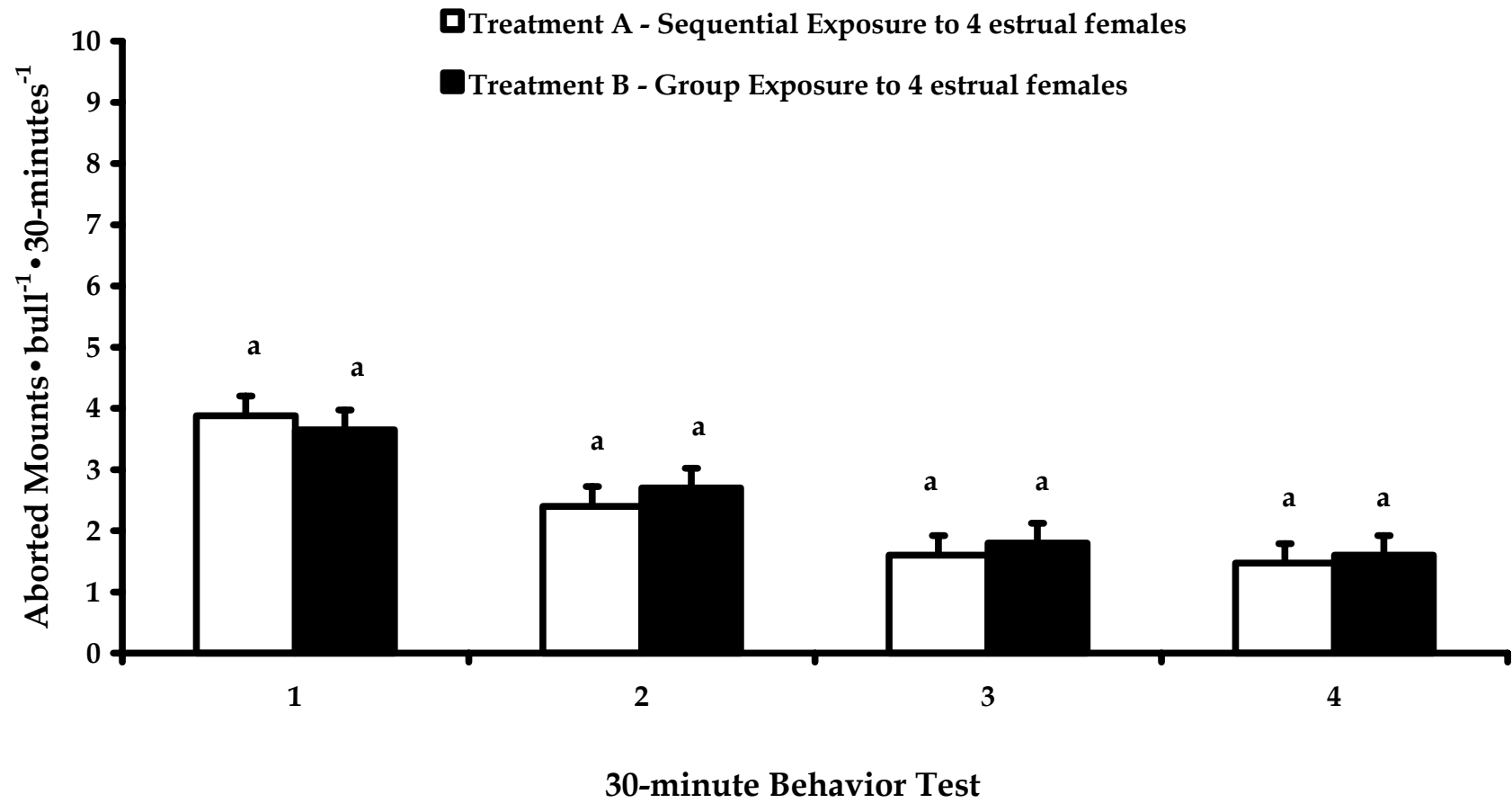


Figure 15. Treatment by time interaction for aborted mounts. Data presented are least square mean aborted mounts•bull⁻¹•30-minutes⁻¹ (\pm SEM) for bulls in Treatments A and B for the 4, 30-minute tests 1, 2, 3, and 4 when bulls were in. Neither treatments nor the treatment x time interaction affected the expression of aborted mounts.

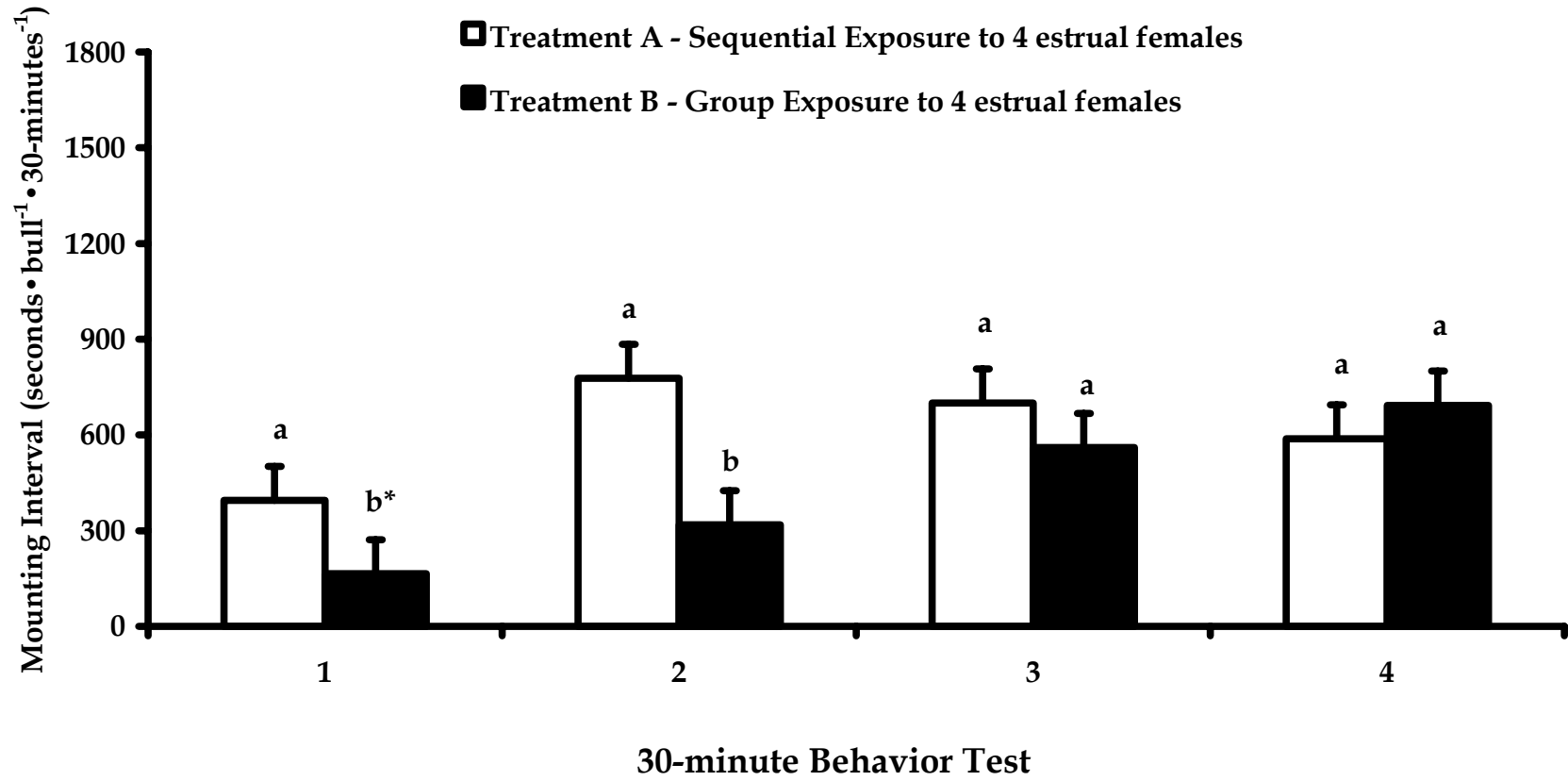


Figure 16. Treatment by time interaction for mounting intervals. Data presented are least square mean mounting intervals in $\text{seconds} \cdot \text{bull}^{-1} \cdot 30\text{-minutes}^{-1}$ (\pm SEM) when bulls were in Treatments A and B for the 4, 30-minute behavior bouts. Least square mean mounting intervals increased in a quadratic manner when bulls were in Treatment A ($P = 0.07$) whereas mounting intervals increased in a linear manner ($P = 0.06$) when bulls were in Treatment B. Least square means with a different superscript within time differ at $P < 0.05$.

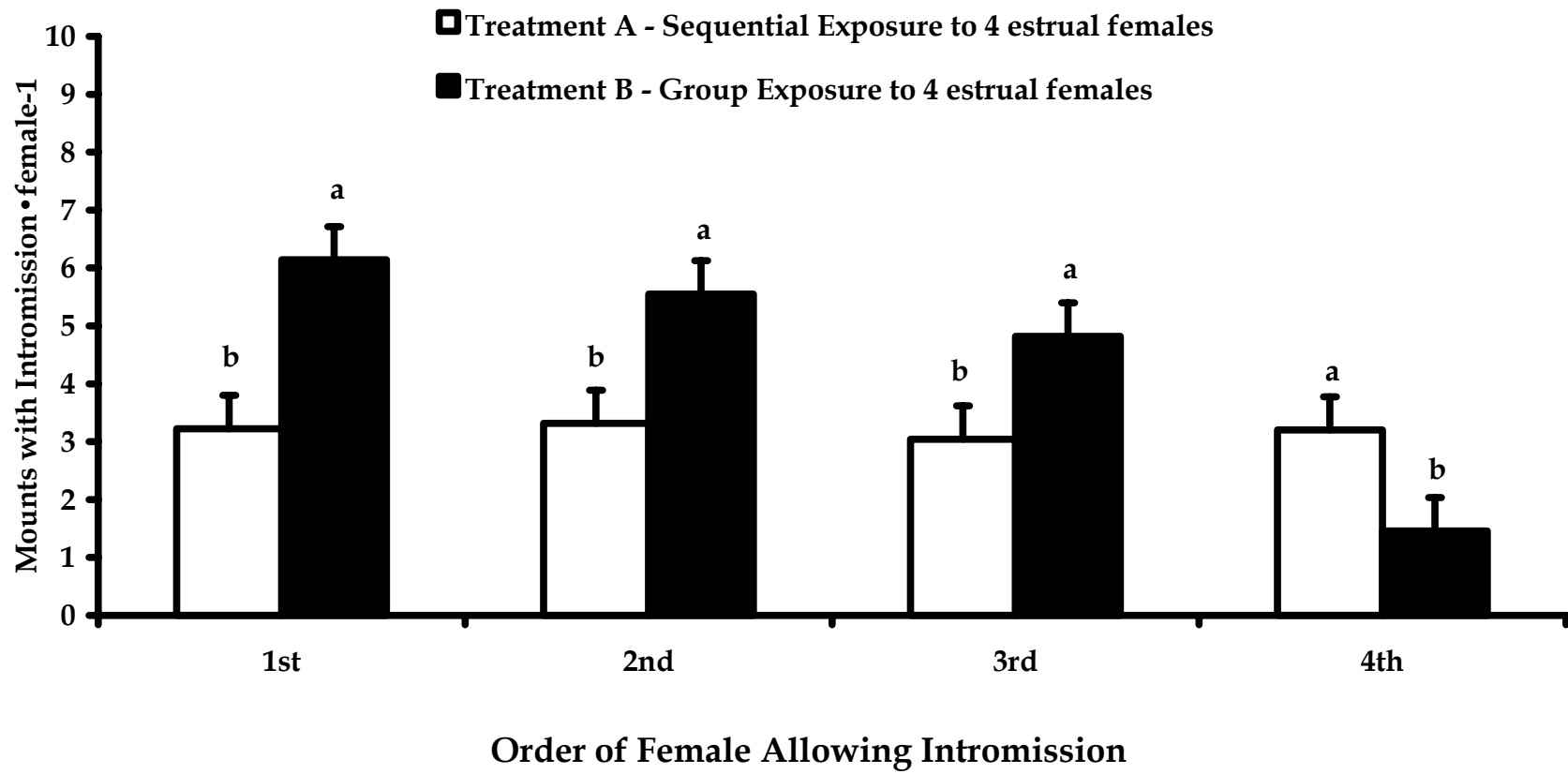


Figure 17. Treatment by female order interaction. Least square mean mounts with intromission•female⁻¹ (\pm SEM) based on the order in which females were copulated with, independent of temporal effects. Least square means with a different superscript within female order differ at $P < 0.05$.

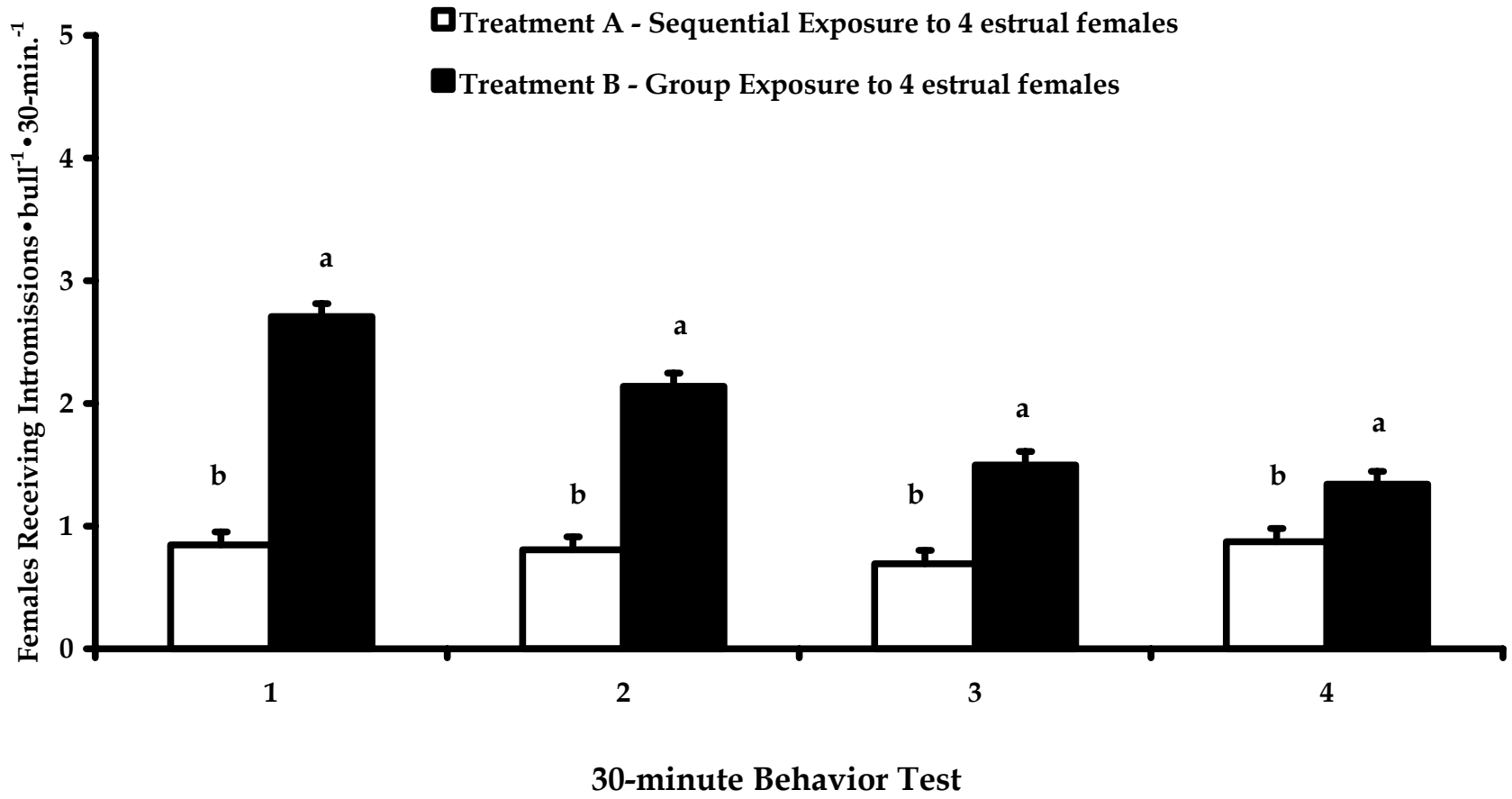


Figure 18. Treatment by time interaction for the number of females receiving mounts with intromission. Data presented are least square mean (\pm SEM) number of females receiving mounts with intromission when bulls were in Treatments A and B for the 4, 30-minute behavior bouts. Number of females receiving mounts with intromission did not change when bulls were in Treatment A, whereas, the number of females receiving mounts with intromission when bulls were in Treatment B decreased in a quadratic manner ($P < 0.001$). Least square means with different superscripts within time are different at $P < 0.05$.

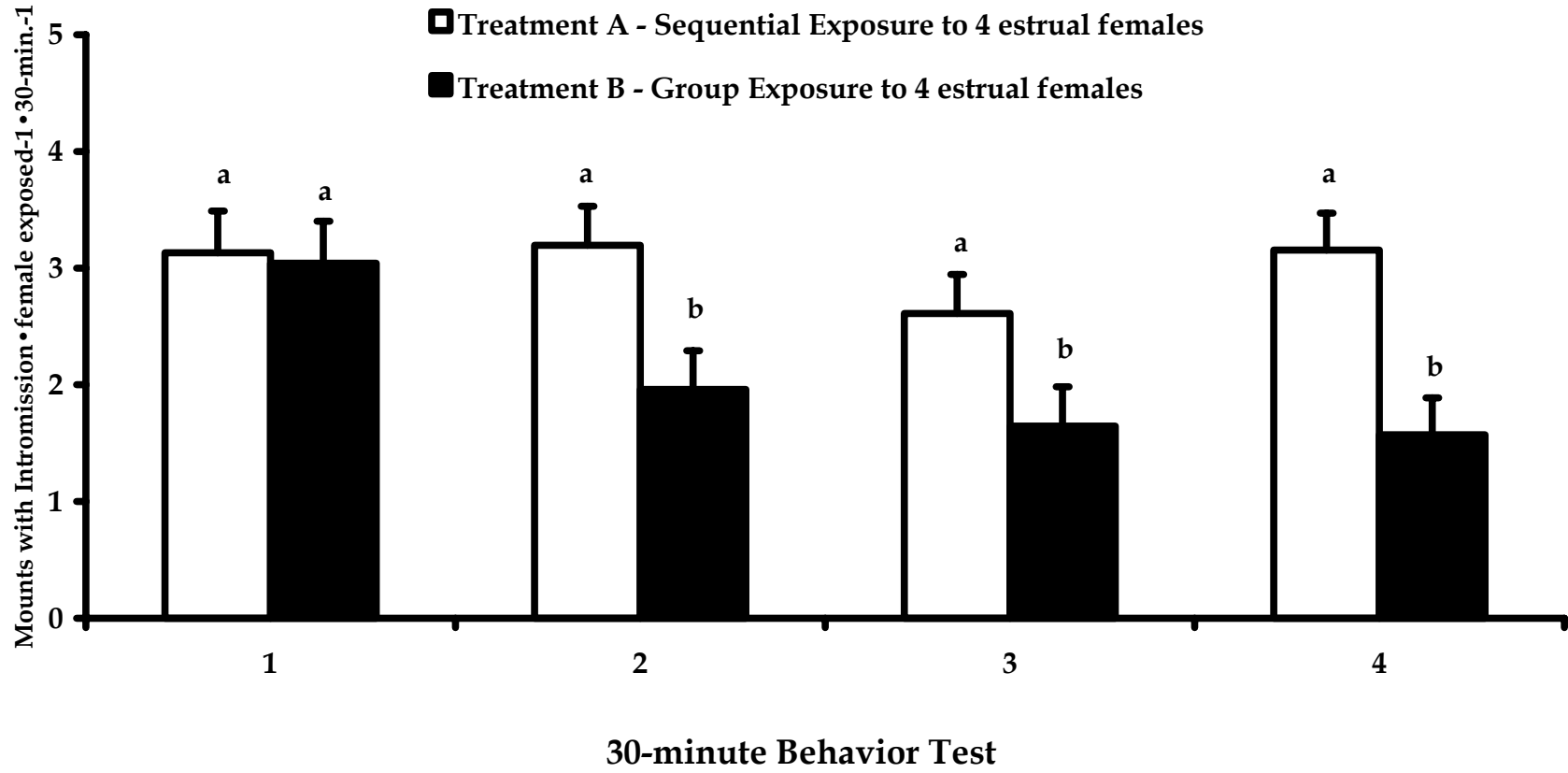


Figure 19. Treatment by time interaction for mounts with intromission per female exposed. Data presented are least square mean (\pm SEM) mounts with intromission per female exposed $\bullet 30\text{-minutes}^{-1}$ when bulls were in Treatments A and B for the 4, 30-minute behavior bouts. Mounts with intromission per female exposed did not change across time when bulls were in Treatment A whereas they decreased in a quadratic manner ($P < 0.01$) when bulls were in Treatment B. Least square means with different superscripts within time are different at $P < 0.05$.

Chapter Four

General Discussion and Conclusions

The present series of experiments demonstrate that the pairing of unrestrained females varying in receptivity and novelty alters consummatory measures of sexual behavior in the sexually experienced, adult bull. Bulls paired with novel, receptive females for 4, 60-minute sexual behavior bouts displayed significantly more total mounts, mounts with intromission and shorter mounting intervals compared with bulls receiving alternating exposure to 2 novel, receptive females, sequential exposure to the same estrual female, or when sequentially paired with a familiar, diestrus female. Bulls paired with 2, novel, estrual females also showed an overall increase in mounting behaviors and consummatory responses, albeit it a somewhat weaker pattern. Males paired with the same estrual female over 4, 60-minute behavior tests showed an inevitable decrease in total mounts, mounts with intromission, and general increase with stability in mounting intervals. Bulls paired with a diestrus female for the 4, 60-minute behavior tests were completely disallowed from exhibiting mounts with intromission although they did continue to attempt mounting sporadically thereafter. Hence, novelty and receptivity of the female stimuli in our paradigm each independently affected male consummatory responses.

Together, these results suggest that female novelty and receptivity dynamically alter consummatory responses in the male bovine by making them more likely to direct bouts of mounting with intromission toward novel, sexually receptive females. An alternative explanation involves the possibility that unrestrained, estrual females who have allowed several bouts of mounting and intromission, differentially solicit further copulations, at least for a time, but may reinitiate solicitation for copulatory behaviors if given some time for rest. Females previously allowing mounts with intromission, and then allowed 60-minutes of rest, showed a general increase in allowing further

copulations, albeit somewhat less than a novel, estrual female who had not been paired with a male. This undoubtedly suggests that female bovine display some level of libido, the underlying motivational aspects of which remain conjecture. It was clear in the first experiment, however, that a novel, estrual female during a third hour of testing was not sufficient in stimulating an increase nor maintaining copulatory response in bulls, as there was a dramatic decrease in total mounts, mounts with intromission with an increase in mounting intervals during this time. This observation would suggest that the Coolidge Effect should be redefined to suggest that sexual satiety in the bull can actually be induced by repeatedly pairing bulls with novel, receptive females for 60-minute sexual behavior bouts. This response has not previously been considered.

The present findings that bull sexual behavior can be altered by systematically pairing unrestrained, variable stimulus females stand in contrast to information cited as justification for conventional methodology used in this field of study (Blockey, 1976b; 1979; 1981a,b,c; Chenoweth et al., 1979; Christensen et al., 1982; Lunstra, 1980; 1986; Coulter and Kozub, 1989; Landeata-Hernandez et al., 2001; Bertram et al., 2002), as females are not considered important participants in sexual behavior and are assumed to have no role in controlling sexual behavior of the bull in “serving capacity” tests. Probably the most important reason for these differences in results is the manner in which each study assesses sexual behavior. The first study assessed the influence of female novelty and receptivity on quantitative measures of sexual behavior, that is, total mounts, mounts with intromission, aborted mounts, mounting intervals and flehmen responses all within the context of an unrestrained, dyadic mating situation. Thus, the types of effects reported here have not been detected directly in studies utilizing restrained females. I do not know whether the procedures used in the first experiment might have produced differential responses under the conventional methodology since I did not use restrained females.

In addition, the testing bout duration was quantitatively different (i.e. 60 minutes) between my first experiment and the traditional “serving capacity” tests, which can range from 5 to 40 minutes (Blockey, 1976b; 1979; 1981a,b,c; Chenoweth et al., 1979;

Christensen et al., 1982; Lunstra, 1980; 1986; Coulter and Kozub, 1989; Landeata-Hernandez et al., 2001; Bertram et al., 2002). One possibility is that a long testing duration could facilitate sexual behavior by increasing arousal or sexual motivation in general, whereas a shorter testing duration might produce conditioned effects on sexual behavior. Studies by Bertram et al. (2002), Boyd et al. (1990), and Lunstra (1986), among others, have reported that bulls undergo a “learning” process when repeatedly tested using the restrained female paradigm, as evidenced by an increase in number of “services”, decreased latency to mounts, etc. Perhaps this “learning” process is really classic Pavlovian (see Pavlov, 1902) conditioning, a factor never considered in the aforementioned research. If this is the case, then the value of these tests in assessing bull sexual behavior seems questionable.

The present findings demonstrate not only the ability of variable female stimuli to produce changes in bull consummatory response but also the utility of testing male sexual behavior in the presence of multiple, unrestrained receptive females. In the second experiment, effects observed on the pattern of copulatory behavior suggested that when allowed to freely interact with 4 unrestrained, estrual females for 2 hours, sexually experienced bulls demonstrated a pattern of sexual motivation consistent with most models of sexual behavior (Pierce et al., 1988; Pfaus, 1996; Agmo, 1999). Namely, several attempted mounts and complete copulations with usually 2-3 of the 4 females for approximately 2, 30-minute bouts followed by a general decrease in copulatory activity, as indicated by a marked decrease in total mounting activity, mounts with intromission, the number of females receiving mounts with intromission, numbers of mounts with intromission per stimulus female exposed, and, finally, a lengthening of mounting intervals. On the other hand, bulls sequentially paired with a single, novel, estrual female every 30 minutes for 2 hours did not show the same mating patterns in most of the sexual behaviors quantified. With the exception of total mounts, when bulls were paired individually with 4, estrual females, they did not show a marked decrease in copulatory activity, specifically, mounts with intromission nor number females receiving mounts with intromission across the 4, 30-minute behavior bouts. Although

aborted mounts decreased in both treatments in a quadratic manner, the ratio of successful mounts with intromission to total mounts (i.e. success ratio) increased when bulls were sequentially paired with 4, estrual females. Surprisingly, this suggests that as the 2-hour test neared completion, bulls in Treatment A became more efficient in distributing mounts with intromission across the remainder of novel, unrestrained females during the remaining 30-minute behavior bouts. When bulls were sequentially paired with 4 novel, unrestrained, estrual females the interval between mounting behaviors did increase by the 2nd 30-minute behavior bout but remained stable thereafter. This contrasts with the linear increase in mounting intervals when bulls were group exposed to 4, estrual females. These results could not have been detected if a conventional test (i.e. “serving capacity” tests) had been used simply because there would be no opportunity for females to interact with males in heterosexual mating scenario. The conventional test strategy, where male subjects are allowed to copulate in groups with restrained females, usually at a 1:1 ratio, might be of interest, but they do not allow direct assessment of copulatory behavioral patterns *per se* but rather are useful in assessing bulls on the basis of sexual performance (i.e. how well the bull copulates with an inanimate object). Furthermore, bovine mating at pasture occurs in groups of free-roaming animals and our group test might represent a more ethologically relevant method of assessing sexual behavior in this species.

Comparison of the results from distribution of mounts with intromissions during sexual behavior testing revealed another unexpected finding. Bulls preferentially distributed mounts with intromission unequally across stimulus females when in a small group. The same was not true when bulls were individually paired with novel, estrual females. When paired with a group of estrual females, bulls seemed to show consistent preference for 3 of the 4 females, based upon the order in which mounts with intromission were allowed. This finding suggests that in group mating situations there are differences in how males distribute mounts and intromissions compared with when presented with stimulus females sequentially. In a study with rats, McClintock (1984) suggested that during a group mating scenario, male rats show a remarkable tendency

to mate with the female that is closest and actively soliciting copulation. Perhaps after repeated copulations with a particular female a bull may become discriminating and choose between potential mates; alternatively, females that have allowed numerous copulations may differentially solicit bulls. Further studies into factors that govern mating interactions should seek to understand the role that mating patterns have in determining the extent to which repeated copulations are distributed among receptive females. This would undoubtedly have effects on bulls' ability to detect and copulate with all estrual females available not to mention ability of subsequent ejaculations to fertilize ova.

In conclusion, enhancing reproductive efficiency of cattle through enhancing sexual behavior of bulls is far from probable. Paradoxically, the need for assessment of bulls' fertility and libido, in light of continued use of estrous synchronization protocols, seems appreciable. Future research in this area should address environmental factors that impact the expression of sexually relevant behaviors, those of which rendered our results lowly repeatable. A test which could reliably predict bulls' copulatory proficiency could aid in understanding factors that impact overall beef herd fertility and possibly lead to management practices that increase reproductive efficiency. The foundation of such a test could be developed by consideration of the research presented in this dissertation.

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Peer Reviewed Publications

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- Target of Opportunity Scholarship, 2000-2001, University of Kentucky
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Society Memberships

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