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Sexual behavior of domesticated ruminants

Larry S. Katz *

Animal Sciences, Rutgers University, 84 Lipman Drive, New Brunswick, NJ 08901, USA

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Abstract

Domesticated ruminants have lived in close association with humans for thousands of years and knowledge of the behavior of these organisms has contributed to their successful domestication, as well as to the management of animals in captivity, both extensive and intensive. Here we describe the reproductive behavioral endocrinology of cattle, goats and sheep. These relatively large and tame animals provide opportunities to conduct a wide range of behavioral studies from short-term to longitudinal or developmental in nature. Highlighted is some of the work from our laboratory describing the social, environmental and endocrine factors that influence the expression of sexual behavior in male and female goats.

Keywords: Sexual behavior; Cattle; Sheep; Goats

Introduction

Animal domestication has been defined by Price (1984) as "that process by which a population of animals becomes adapted to humans and to the captive environment by some combination of genetic changes occurring over generations and environmentally induced developmental events recurring during each generation." Genetic changes associated with animal domestication include: inbreeding, which results in increased homogeneity; genetic drift, in which genes may be fixed by chance in a small population; artificial selection, either deliberate or unintended (i.e., when genes for selected traits are closely linked to genes for other traits); and natural selection in captivity, which is all of the selection influencing captive animals not accounted for by artificial selection (Price, 1984). For those who study the behavior of domesticated livestock in particular, an intriguing problem arises as a result of the genetic changes from what Price described as 'relaxation of natural selection' (Price, 1984). This concept implies that some behaviors lose their adaptive significance in the captive environment. For example, livestock producers generally breed animals in what is known as single-sire groups, i.e., one male with multiple females for the duration of the breeding season. This permits all selected males, even those with low libido, equal opportunity to produce offspring. The heritability of serving capacity, a measure of mating competence, has been estimated to be 0.59 (Blockey et al., 1978). Permitting animals with low libido to reproduce without competition from males with high libido has thus increased the quantitative variation in sexual performance, the combination of mating competence and sexual motivation. Indeed, it is estimated that eight to 10% of male cattle and perhaps as many as 15 to 25% of male sheep have low sexual performance (Price, 1985). This phenomenon has stimulated basic and applied research on sexual behavior in male ruminants in ours and many other laboratories around the world. Many of the studies have focused on the endocrinology of the male describing the role of various hormones in the regulation of the development of sexual behavior, characterizing the influence of hormones on the adult expression of sexual behavior, or quantifying the concentrations of various hormones in an attempt to predict the sexual performance of potential herd sires. This latter rationale for behavior studies is based on the negative economic impact of low performing males producing either fewer offspring or offspring conceived late in the breeding season, as these males may not breed all the herd females at the first estrus of the season. As weaned animals are generally sold as a group at one time, younger animals are lighter in weight and therefore produce lower returns.

* Fax: +1 732 932 6996.
E-mail address: katz@aesop.rutgers.edu.

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The historic rationale for studying the behavioral endocrinology of female ruminants, especially cattle, was based on the need for humans to detect estrus as part of artificial insemination programs. Some of these applied questions have been addressed or partially resolved with induced ovulation protocols that simplify or eliminate the need for estrus detection or electronic detection systems that automatically record changes in the estrus-related physical activity of females. Nevertheless, basic questions regarding sexual differentiation and sex dimorphism, or lack thereof, warrant vigorous study of attractivity, proceptivity and receptivity in female ruminants.

Males

Development

Mounting, both male-oriented and female-oriented, occurs at a very early age in males (Hafez and Bouissou, 1975). For example, at 2 months of age, if implanted with testosterone and estradiol benzoate, steers (castrated males) will display mounting behavior (Lesmeister and Ellington, 1977). At 4 and 6 months of age, intact bulls mount regularly (Wolf et al., 1965; Bass et al., 1977). At these prepubertal ages the expression of mounting behavior may not be entirely dependent upon gonadal steroid hormones as Folman and Volcani (1966) observed 9 of 12 prepubertally castrated animals repeatedly mount an estrus female. This lack of testosterone dependence for mounting behavior was also demonstrated for sexually experienced males (Imwalle and Schillo, 2002). However, quantitative differences in mounting behavior between steers either treated or not treated with steroid hormones do exist (Lesmeister and Ellington, 1977; Dykeman et al., 1982). Generally, castration decreases the frequency of sexual behavior in ruminants, and administration of exogenous testosterone to the castrated animal restores sexual behavior in sheep (Clegg et al., 1969), goats (Hart and Jones, 1975), and red deer (Lincoln et al., 1972).

Steroid hormone replacement

Other studies have examined the effects of testosterone as well as other androgens and estradiol treatments on reproductive behavior in sheep (D'Occhio and Brooks, 1980, 1982; Pinckard et al., 2000; Parrott and Baldwin, 1984; Parrott, 1978) and cattle (Dykeman et al., 1982). However, minimum dose requirements to activate male sexual behavior in sexually inexperienced animals have not been determined for most species studied. At subthreshold doses, testosterone has been shown to facilitate sexual behavior in a dose response manner in monkeys (Michael et al., 1984; Phoenix and Chambers, 1986; Zumpe and Michael, 1985), rats (Damassa et al., 1977; Hlinak et al., 1979), and sheep (D'Occhio and Brooks, 1982; Sanford et al., 1972). Studies in cattle that did not reveal a dose response (Foote et al., 1976; Price et al., 1986) failed to examine sub-physiological doses of testosterone. Prior studies have also used adult or sexually experienced males.

We investigated the facilitation of reproductive behavior by testosterone in the sexually inexperienced, castrated male goat (McMunn and Katz, 2001). The objective of the study was to determine the behavioral response of sexually inexperienced, castrated male goats to different physiological doses of testosterone and to determine if testosterone facilitation of sexual behavior in this species occurs in a dose response manner. Males were castrated at 8–14 months of age. At 18–24 months old they were implanted subcutaneously with 2 cholesterol implants (C) or 2, 4, or 8 testosterone implants (2T, 4T or 8T, respectively). During the time implants were in place serum T concentration averaged 64 ± 8, 456 ± 14, 738 ± 39, and 1333 ± 84 pg/ml for the C, 2T, 4T, and 8T groups, respectively. Serum testosterone concentrations increased by 32 h after implants were inserted, and decreased by 32 h after implant removal. Serum testosterone concentrations in goats in the 2T treatment were similar to reported non-breeding season concentrations of testosterone, while the 8T treatment is consistent with the lower range of breeding season concentrations in this species (Perez Llano and Mateos Rex, 1994). Behavior was assessed weekly in sexual performance tests. Sexual performance tests of 15-min duration were conducted in $2\text{ M} \times 2\text{ M}$ pens with one male and one sexually receptive female. Behaviors were averaged over three time periods: pretreatment, during treatment with steroid implants, and post-treatment. There were no significant differences among groups in mounting frequency during any time period, although during the period when the implants were present the 8T group performed significantly more sexual behaviors (all sexual behaviors combined) than the C group. There were tendencies for most sexual behaviors to increase with increasing number of testosterone implants, suggesting a dose response. However, as frequencies of all behaviors were low, group sizes may not have been adequate to verify this effect. Continuous release of testosterone may not be optimal for initiation of sexual behavior in sexually inexperienced animals. The episodic release of testosterone may be required for the initial exhibition of normal mounting and ejaculatory behaviors at puberty. The inexperienced rams in the study by D'Occhio and Brooks (1982) did respond to treatment with testosterone propionate injections daily, with mounting and ejaculatory behaviors exhibited. Our study examined the development of sexual behavior in inexperienced males treated with exogenous testosterone and was different from many previous studies in the use of sexually inexperienced males. As the dose of testosterone required for restoration of sexual behavior in castrated males is higher than that necessary for maintenance of sexual behavior (Damassa et al., 1977), so may the dose of testosterone required for initiation of sexual behavior in inexperienced males be higher than that required for restoration or maintenance.

Attempts to correlate sexual activity in male ruminants with circulating concentrations of reproductive hormones have revealed little meaningful relationship. Foote et al. (1976) found no relationship between testosterone concentrations and subjective evaluations of willingness to ejaculate into an artificial vagina in Holstein bulls, a dairy breed. Similar lack of correlation between either testosterone or luteinizing hormone (LH) concentrations and various measures of sexual behavior were reported for other cattle breeds as well (Chenoweth et al., 1979; Lunstra et al., 1978; Price et al., 1986).