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Differential effects of androgens, estrogens and socio-sexual context on sexual behaviors in the castrated male goat

William F. Fritz Jr., Lena S. Sena, Susan E. Becker, Larry S. Katz*

Rutgers University, New Brunswick, NJ, USA

ABSTRACT

The behavioral and endocrine activation of sexual behaviors exhibited by male goats, especially self-enurination (SE), is poorly understood. In the first experiment, to assess the influence of socio-sexual context on SE in bucks, the effects of distance from does, the presence of estrous versus non-estrous does and the presence of another buck on SE and courtship frequencies of intact male goats (bucks; $n = 12$) were tested using a unique behavior test apparatus. For experiments 2 and 3, to test the relative contributions of sex steroid hormones and socio-sexual context on SE, castrated male goats (wethers; $n = 20$) were randomly divided into five groups and injected for seven weeks with one of the following: 25 mg testosterone propionate (T), 25 mg dihydrotestosterone propionate (DHT), 100 μg estradiol benzoate (E), 100 μg E and 25 mg DHT (E + DHT), or oil (CON). The effects of these treatments on frequency of SE and courtship were assessed using the behavior test apparatus (social scenarios) adapted from the findings in experiment 1. In one scenario, a wether could observe (from 4.6 m) a buck and estrous female (doe) together in a wire mesh holding pen. In a different scenario, the wether could observe (from the same distance) a buck that could only court the estrous doe through a wire mesh barrier. Finally, to observe the effects of steroid treatment on mounting and ejaculation frequencies, in addition to SE and courtship, each wether was placed in a pen with an estrous doe for 10 min. After a five-week, treatment-washout period, wethers were randomly assigned to different treatment groups and retested. In experiment 1, bucks that were distanced from females displayed more SEs than those with fence-line contact, while those with fence-line contact displayed more bouts of courtship ($P < 0.05$). In experiments 2 and 3, courtship frequencies displayed in all three scenarios were greater than CON only for groups exposed to estrogen directly or via aromatization (T, E + DHT, E; $P < 0.05$). Frequencies of SE exhibited during behavior tests in which the wether was watching were greater than CON only for androgen-treated groups (T, E + DHT, DHT; $P < 0.05$). In contrast, when the wether was free to interact with the female, only the DHT group displayed SE at a higher frequency than CON ($P < 0.05$). Treatment had no effect on mount frequencies in this test scenario, however ejaculation frequencies were highest for T and E + DHT ($P < 0.05$). These studies suggest that the courtship behaviors of the male goat are estrogen-dependent. However, SE appears to be activated by androgens. It was also demonstrated that social context contributes as much to behavior expression as steroid treatment, as in social scenario 2 some sexual behaviors were displayed in similar frequencies across groups, despite differing sex steroid treatments.

1. Introduction

In the domesticated male goat (buck), testosterone (T) rises at the onset of the breeding season, and falls several months later (Delgadillo et al., 2004; Muduuli et al., 1979; Walkden-Brown et al., 1994). Coinciding with this increase, the buck displays sexual behaviors at a higher frequency than in the non-breeding season (Hart and Jones, 1975). These behaviors include courtship behaviors such as tongue flicks, foreleg kicks, snorts, vocalizations, or any combination of these, as well as mounting and self-enurination (SE).

Self-enurination is characterized by turning the head and shoulders downwards towards the hindquarters and emitting urine from the erect penis onto the face, beard and front legs (Fig. 1). The urine is delivered in a manner ranging from a spray to a narrow stream, and can be released in short pulses or in a continuous, steady flow. Self-enurination frequently includes the buck lapping his urine and may conclude with the goat grooming the penis with his tongue and the flehmen response.

The adaptive value of SE to the buck remains unclear though several hypotheses exist. In several studied species, male-typical sexual behaviors including scent marking are regulated by T, suggesting such behaviors serve reproductive functions (Bronson and Whitten, 1968; Ferkin et al., 1994; Hau, 2007; Yahr et al., 1979). Further, the presence of an erection and the increase in the behavior's frequency in the presence of females also suggest a reproductive function. Experiments in our lab have sought to demonstrate the most popular hypothesis that SE is used to attract estrous females. While estrous females seem to prefer buck urine compared to prepubertally castrated male (wether) urine (unpublished data), this may not be the only function of the behavior.

Findings presented by Price et al. (1986) suggest that the behavior is more likely to occur when the buck can view, but not breed an estrous female. This is in agreement with observations in our lab that the behavior most often occurs when the buck is separated from a female by a fence, or when the buck is in the post-ejaculatory refractory period. It was also found that distance from the stimulus and the presence of

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* Corresponding author at: 88 Lipman Drive, New Brunswick, NJ 08901, USA.
E-mail address: lskatz@rutgers.edu (L.S. Katz).

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Fig. 1. Buck exhibiting self-enurination.

another buck (especially when that buck is tending the female) increase the likelihood of SE, perhaps suggesting that "frustration" of the sex drive may increase the likelihood of the behavior (Price et al., 1986). These findings were used to design behavioral test scenarios to increase the likelihood of SE, which is ordinarily displayed with relatively low frequency.

The activation of sexual behaviors by T in the male goat and many other species has been demonstrated extensively (Alsum and Goy, 1974; Beyer et al., 1975; Damassa et al., 1977; DeBold and Clemens, 1978; Harding et al., 1983; Hart and Jones, 1975; Katz, 2007; Lincoln et al., 1972; Schumacher and Balthazart, 1983). However, the aromatization or reduction of T to estrogens or other androgens, respectively, accounts for most of the hormone's observed effects on the male's sexual behaviors in bovid species (D'occhio and Brooks, 1980; Dykeman et al., 1982; Parrott, 1978). The relative contribution of androgens and estrogens to the activation of specific sexual behaviors may vary greatly across species. In sheep and cattle, which are in the same biological family (Bovidae) as goats, activation of sexual behaviors is estrogen-dependent (D'occhio and Brooks, 1980; Dykeman et al., 1982; Parrott, 1978). In some species, activation of sexual behaviors is androgen-dependent, or a combination of androgen- and estrogen-dependent. For example, in the guinea pig only androgens activate sexual behavior (Alsum and Goy, 1974). In the rabbit (Beyer et al., 1975) and zebra finch (Harding et al., 1983), both androgens and estrogens are needed to activate sexual behaviors. In other species, such as the hamster, both androgens and estrogens independently activate certain sexual behaviors (DeBold and Clemens, 1978). In the male goat, the study of the effect of sex hormones on male sexual behavior has been limited to testosterone. The endocrine activation of SE has not been studied.

The objective of the first study (Experiment 1: Effects of social scenario on SE and courtship in bucks) was to determine the environmental conditions (specifically socio-sexual) that increase the likelihood of SE. Findings from this study were used for the subsequent experiments in which we measured the relative contributions of androgen (non-aromatizable), estrogen and external cues on the frequency of sexual behaviors in hormone-treated prebubertally castrated males (wethers). In the second experiment (Experiment 2: Hormones and social scenario affect sexual behaviors in wethers), the effect of the aforementioned hormones on the frequency of SE was addressed using the social scenarios derived from experiment 1. For experiment 1, it was hypothesized that the presence of estrous does, the inability to directly interact with estrous does, and the presence of another buck that was able to interact with estrous does would increase the likelihood of self-enurination in bucks. For experiment 2, it was hypothesized that both socio-sexual context and circulating sex steroid concentrations influence the frequency of self-enurinations in wethers. More specifically, treatment of wethers with estrogen and their placement in a scenario in which they were able to watch, from a distance, another buck interact freely with an estrous doe, would increase the probability of self-enurination.

2. Materials and methods

2.1. Animals

All animals were Alpine goats between the ages of 2–9 years, and received a diet consisting of grass hay and grain, and had ad libitum access to water and mineral salt blocks. Diet and husbandry was in compliance with the Consortium Guide for the Care and Use of Agricultural Animals in Agricultural Research and Education (FASS, 2010). Research was conducted as approved by the Rutgers University Animal Care and Facilities Committee. Male and female goats were housed on the NJ Agricultural Experiment Station Research Farm in New Brunswick, NJ (40°29′10″N/74°27′8″W) in barns with free access to outdoor exercise areas. Experiment 1 was conducted during the 2012 breeding season and experiment 2 was conducted during the 2014 breeding season, which for Alpine goat begins in mid-August and terminates near the end of January in the northern hemisphere. Focal goats in experiment 1 were gonadally intact males (bucks; n = 12). Stimulus estrous females were estrus-synchronized intact females (does; n = 14) and stimulus non-estrous females were ovariectomized females (OVX does; n = 6). In experiment 2, focal goats were prepubertally castrated males (wethers; n = 20). Teaser bucks (n = 3) were gonadally intact males and stimulus females were estrus-synchronized intact does (n = 24) or estrus-induced OVX does (n = 8).

2.2. Hormone treatment

Subject wethers in experiment 2 were randomly divided into five treatment groups, controlling for age. Each group was injected subcutaneously three times weekly, for eight weeks, with one of the following; sesame oil (vehicle control; CON), 25 mg testosterone propionate (T), 100 μg estradiol benzoate (E), 25 mg dihydrotestosterone propionate (DHT), and a mixture of 100 μg estradiol benzoate and 25 mg dihydrotestosterone (E + DHT). After a five-week washout period, wethers were randomly reassigned to new treatment groups and injected for another eight weeks. Assignment of wethers to treatment groups was balanced for weight and age. The range of bodyweights and ages across treatments were 73.1 to 73.4 Kg and 4.8 to 5.5 y, respectively.

2.3. Estrus synchronization

Estrus-synchronized stimulus does in experiment 1 were drawn from a herd of 14 and estrus-induced or synchronized stimuli does in experiment 2 were drawn from a herd of 8 and 24, respectively. The herds were divided into two groups, which were estrus-induced or synchronized on alternating weeks. For experiments conducted as females entered the breeding season, estrus was induced in OVX females by providing exogenous progestins and estradiol from the protocol developed by Billings and Katz (1997). Estrus synchronization in the intact herd was accomplished using a sequential treatment of prostaglandin (PGF2α). During the breeding season each female received an injection of 10 mg PGF2α (dinoprost tromethamine, i.m.) 60 h prior to preference test as modified from Ott et al. (1980). Standing estrus was detected prior to each behavior test. A non-experimental buck was brought into the females' home pen and allowed to mount females but not allowed to intromit. If the female stood to be mounted, she was considered to be in estrus. If the female rejected the male, she was considered non-estrous.

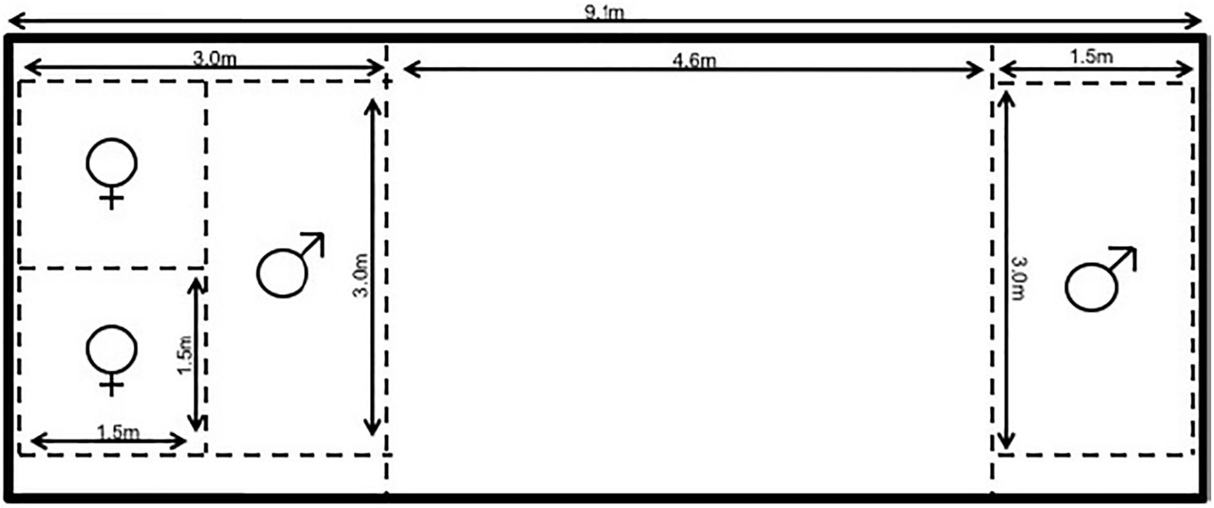

Fig. 2. Behavior test apparatus for experiment 1: Stimulus does were placed at one end of the apparatus, in separate pens. Depending on the test conditions, a buck was either "alone" or "paired" with a buck in the opposite male pen. A buck in the "far" pen was 6.1 m from stimulus does and in the "near" pen had fenceline contact with does. Observations were made through a fence barrier in the aisle adjacent to the lower barrier in the diagram.

2.4. Behavior testing

2.4.1. Experiment 1: effects of social scenario (SS) on SE and courtship in bucks

In experiment 1, a 5-min behavior test was used to assess the contributions of distance from stimulus does, the presence of another buck and the estrous state of stimulus does on the frequency of SE and courtship in bucks (Fig. 2). Each buck was tested in all eight possible combinations of the following conditions; in the pen 6.1 m from stimulus does (far), in the pen with fence-line contact with stimulus does (near), with another buck in the opposite buck pen (paired), without a buck in the opposite buck pen (alone), with estrous stimulus does (estrous does) or with non-estrous stimulus does (non-estrous does). Thus, the eight conditions were; 1) Far, paired, estrous does, 2) Far, paired, non-estrous does, 3) Far, alone, estrous does, 4) Far, alone, non-estrous does, 5) Near, paired estrous does, 6) Near, paired, non-estrous does, 7) Near, alone, estrous does, 8) Near, alone, non-estrous does. Total bouts of courtship and total number of SEs were recorded for each buck in each of his eight, 5-min tests.

2.4.2. Experiment 2: hormones and social scenario affect sexual behaviors in wethers

At the end of each 8-week course of steroid treatment, wethers were tested in three 10-min social scenarios. In social scenarios 1a and 1b, the test wether had no access to a female and was watching the female from a distance of 4.6 m. In 1a, the wether watched a buck courting and mounting an estrous female, and in 1b, he watched a buck courting an estrous female through a fence barrier, thus no mounting occurred. In social scenario 2, the test wether was allowed to interact freely with an estrous female for the duration of the test. In all social scenarios, SE and courtship frequencies were recorded. In Scenario 2, in addition to SE and courtship, mount and ejaculation frequencies were also recorded.

Social Scenario 1A	Subject wether watched a buck courting and mounting an estrous female
Social Scenario 1B	Subject wether watched a buck courting an estrous female through a fence barrier
Social Scenario 2	Wether was allowed to interact freely with an estrous female

2.5. Statistical analysis

2.5.1. Experiment 1: effects of social scenario on SE and courtship in bucks

In experiment 1, the effect of three conditions (distance from stimulus does, presence of another buck, and estrous state of stimulus does) were assessed for SE and courtship frequencies. Courtship and SE frequencies from each buck, tested four times for each comparison, were combined (ignoring the other two conditions), as overall frequencies were relatively low. For example, to assess the effect of distance from stimulus does on SE, the SE frequency for bucks in the far pen from tests where he was 1) alone with estrous does, 2) alone with non-estrous does, 3) paired with estrous does and 4) paired with non-estrous does were summed and divided by the total number of SEs in all eight conditions (SEs in near and far pens combined). This generated a proportion of SEs occurring in the far pen to SEs occurring in both the near and far pens. Combined frequencies of SE and proportion of bucks displaying SE for each of the three conditions were analyzed by chi-squared test to determine if frequencies differed from chance (50%). Differences were deemed significant at $P < 0.05$.

2.5.2. Experiment 2: hormones and social scenario affect sexual behaviors in wethers

Mean SE frequencies in social scenarios 1 and 2 and mean courtship frequencies, in social scenario 2 underwent SQRT$(x + 1)$ transformation before analysis. These and all other behavior frequencies, except courtship frequency in social scenario 1, were analyzed by one-way analysis of variance (ANOVA) and mean behavior frequencies between treatments were compared using Bonferroni's Multiple-Comparison Test. Cohen's f test was used to calculate effect size comparing within and between variance. Treatment effect was deemed significant at $P < 0.05$. Since courtship frequencies in social scenario 1 were highly variable among individuals, these data were not normally distributed. These data were thus analyzed by Welch's test of means allowing for unequal variances and medians were compared by Kruskal-Wallis Multiple-Comparison Z-value test. Differences between treatments were compared by Dunn's test and deemed significant at $Z > 1.96$.

3. Results

3.1. Experiment 1: effects of social scenario on SE and courtship in bucks

Table 1 displays total SE frequencies for the 12 bucks in each of the eight conditions. In this experiment, more total SEs occurred in the far

Table 1
Self-enurinations more likely to occur in bucks distanced from does: Sum of self-enurinations and number of bucks that displayed self-enurination during a 5-min test (n = 12). Far bucks were 6.1 m away from and near bucks had fenceline contact with stimulus does. Bucks were alone when they were the only buck in the apparatus and paired when another buck was in the opposite pen (near or far). Stimulus does were estrous or non-estrous.

Buck condition	Sum of SEs/ 5 min	Sum of bucks displaying SE
Far, Alone, Estrous does	4	3
Far, Alone, Non-estrous does	3	3
Far, Paired, Estrous does	6	4
Far, Paired, Non-estrous does	4	4
Near, Alone, Estrous Does	2	2
Near, Alone, Non-estrous does	1	1
Near, Paired, Estrous does	2	1
Near, Paired, Non-estrous does	2	2

pen (17/24; 71%), than were displayed in the near pen (7/24; 29%; $\chi^2 = 8.3$; $P = 0.004$). Of the instances in which a buck was in the far pen, SE was displayed in 14/48 (29%) of tests and when they were in the near pen, it was displayed in 6/48 (13%) of tests ($\chi^2 = 4.0$; $P = 0.04$). SEs occurred in 14/24 (58%) of tests when the buck was in the apparatus with another buck in the opposite buck pen and 10/24 (42%) occurred when he was alone ($\chi^2 = 1.3$; $P = 0.25$). Of the tests in which a buck was in the apparatus with another buck present, there were SEs in 11/48 (23%) of tests and 9/48 (19%) of tests when the buck was alone ($\chi^2 = 0.25$; $P = 0.62$). Display of SE was not affected by estrous-state of the stimulus females ($\chi^2 = 1.3$; $P = 0.25$).When estrous does were used as the stimulus, 14/24 (58%) of the total number of SEs were recorded and SE was displayed in 10/48 (21%) of tests. When non-estrous does served as the stimulus, 10/24 (42%) of total SEs were displayed and in 10/48 (21%) of tests SE occurred.

Table 2 displays total courtship frequencies for the 12 bucks in each of the eight conditions. For courtship, as expected, more courtships occurred in the near pen (1570/1618; 97%) than in the far pen (48/1618; 3%; $\chi^2 = 2863.4$; $P < 0.00001$). In tests in which the buck was in the near pen, bucks displayed courtship in more tests (44/48; 92%), than they did in tests in the far pen (7/48; 15%; $\chi^2 = 57.3$; $P < 0.00001$). When the stimulus does were in estrous, bucks displayed courtship in higher frequencies (1227/1618; 76%) than in the presence of non-estrous does (391/1618; 24%; $\chi^2 = 863.9$; $P < 0.00001$). However, the number of tests in which bucks displayed courtship when does were in estrus was not greater (28/48; 58%) than the number of tests where bucks displayed courtship in the presence of non-estrous does (25/48; 58%). The presence of another buck in the apparatus did not have an effect on the total number of courts (815/1618; 50%) when compared to total courts when bucks were alone (803/1618; 50%). There was no difference on the number of bucks that displayed courtship in tests in which they were with another buck (25/48; 52%) when compared to being in the apparatus alone (28/48; 58%).

Table 2
Courtship occurs at higher frequencies in bucks with fenceline contact with does: Sum of courtships (CT) and number of bucks that displayed courtship during a 5-min test (n = 12). Far bucks were 6.1 m away from and near bucks had fenceline contact with stimulus does. Bucks were alone when they were the only buck in the apparatus and paired when another buck was in the opposite pen (near or far). Stimulus does were estrous or non-estrous.

Buck condition	Sum of CTs/ 5 min	Sum of bucks displaying CT
Far, Alone, Estrous does	33	3
Far, Alone, Non-estrous does	6	2
Far, Paired, Estrous does	3	2
Far, Paired, Non-estrous does	6	2
Near, Alone, Estrous Does	545	12
Near, Alone, Non-estrous does	219	11
Near, Paired, Estrous does	646	11
Near, Paired, Non-estrous does	160	10

3.2. *Experiment 2: hormones and social scenario affect sexual behaviors in wethers*

3.2.1. *Social scenarios 1A and 1B*

Results from social scenario 1A and 1B were combined for analysis, as their results did not differ. Cohen's f statistic for effect size was 0.41. In both scenarios, wethers treated with T, E, and E + DHT courted more frequently than CON- or DHT-treated wethers (Fig. 3; $P < 0.05$). Wethers treated with T, DHT, and E + DHT exhibited SE more frequently than CON- or E-treated wethers (Fig. 4; $P < 0.05$). In summary, groups whose treatments contained E or T, which is aromatized to estradiol, courted at higher frequency than CON- or DHT-treated wethers. Groups whose treatments contained androgen exhibited SE in greater frequency than those treated with CON or E only.

3.2.2. *Social scenario 2*

In social scenario 2, wethers treated with T, E, and E + DHT displayed courtship in higher frequency than CON wethers or those treated with DHT (Fig. 5; $P < 0.05$). Wethers treated with DHT were the only group to display SE in greater frequency than CON (Fig. 6; $P < 0.05$). No differences between treatment groups for mount frequencies were observed (Fig. 7). Only wethers treated with T and E + DHT exhibited ejaculations in greater frequency than CON (Fig. 8; $P < 0.05$).

4. Discussion

The goat provides a unique model for the study of sexual behavior, in part, because it has been subjected to thousands of years of domestication. For those behaviors in which human intervention overcomes natural selection pressure, domestication can “relax” said pressure on some behaviors, possibly resulting in a loss of adaptive significance (Price and Smith, 1984). This makes assessing the contexts in which behaviors occur and understanding the selective processes contributing to the expression of behavior in the goat both difficult and interesting.

The sexual behaviors of the male goat are dependent upon highly complex interactions between his internal and external environment. It is, of course, both the buck's internal and external environments that influence behaviors via highly complex interactions. This experiment expands upon how these factors (particularly endocrine profile and social environment) influence the activation and frequency of sexual behaviors in the male goat.

In a seasonal breeder, such as the male goat, circulating T concentrations increase during the breeding season, causing behavioral changes that facilitate courtship and copulation (Delgadillo et al., 2004; Longpre et al., 2011; Walkden-Brown et al., 1994; Walkden-Brown et al., 1997). However, there is significant variation in the degree of and duration to cessation of sexual behaviors following castration. In goats, though obvious decreases in sexual behaviors are noted within a few weeks following castration, the ejaculatory response may remain for over a year following castration. Courtship and mounting, though diminished in frequency soon after castration, may still be presented occasionally throughout the lifespan, even if the castration is performed prior to puberty (Hart and Jones, 1975). These findings were consistent with our finding that sexual behaviors were displayed by CON wethers in this experiment.

Similar to other bovids, courtship behaviors in the male goat were activated by estrogens, regardless of the social scenario presented. While the non-aromatizable androgen DHT has been shown to increase sebaceous gland secretions in the goat buck (Iwata et al., 2000), results from this study show that it also activates SE. This finding suggests that the behavior evolved for the purpose of scent marking because in

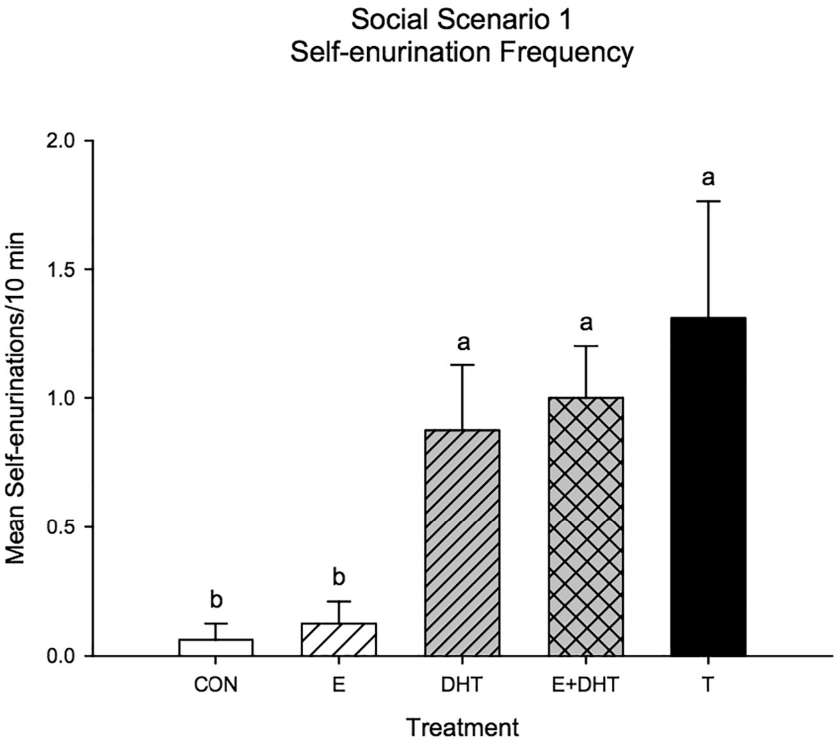

Fig. 3. Androgens activate self-enurination: Self-enurination frequency (Mean ± SEM) displayed by the wethers treated with CON (vehicle control), T (testosterone propionate), E + DHT (estradiol benzoate + dihydrotestosterone propionate), E (estradiol benzoate), and DHT (dihydrotestosterone propionate) during a 10-min test. In social scenario 1, wethers watched stimulus from 4.6 m. For each treatment, n = 8. Bars with different superscripts differ ($P < 0.05$).

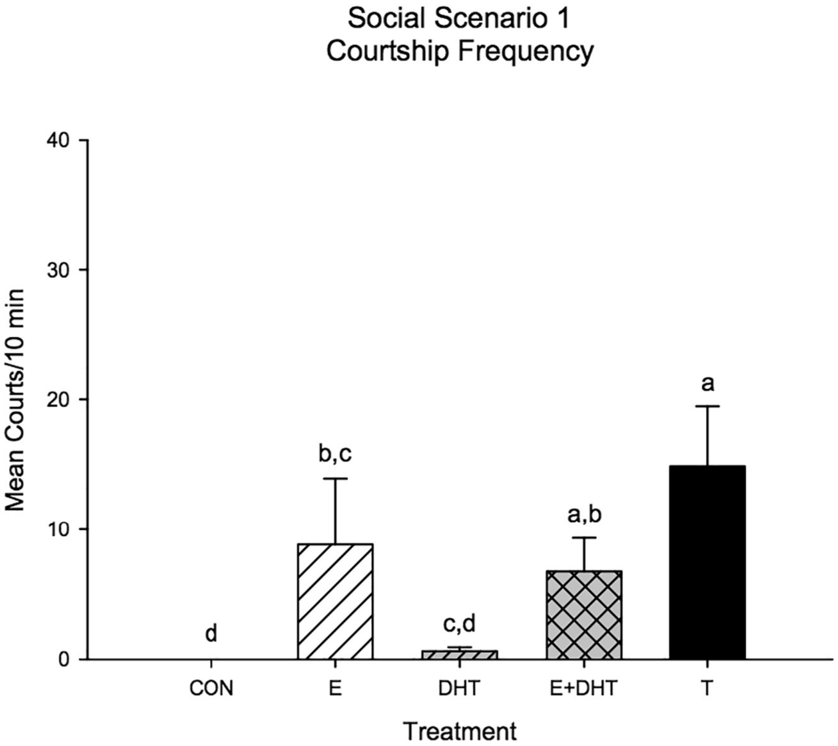

Fig. 4. Estrogens activate courtship: Courtship frequency (mean ± SEM) displayed by the wethers treated with CON (vehicle control), T (testosterone propionate), E + DHT (estradiol benzoate + dihydrotestosterone propionate), E (estradiol benzoate), and DHT (dihydrotestosterone propionate) during a 10-min test. In social scenario 1, wethers watched stimulus from 4.6 m. For each treatment n = 8. Bars with different superscripts differ ($P < 0.05$).

several related species, scent marking behaviors are androgen-dependent. Prior to this study, the relative roles of estrogens and non-aromatizable androgens in the activation of SE had not been studied. It has been shown in sheep and cattle, that appetitive sexual behaviors are activated by estrogens aromatized from T. Activation of SE by a non-aromatizable androgen is a unique finding and suggests that SE is not a typical appetitive sexual behavior even though it is associated with sexual arousal (Price et al., 1986).

Clarke et al. (1976) conducted a study comparing the effects of T delivered to ewes at different times during pregnancy on sexual behaviors of the offspring. Interestingly, though offspring of ewes treated with T prior to 90 days of gestation displayed a male-like urination posture (standing normally, voiding urine in pulses), they found that ewe lambs exposed to T from day 90 to 140 of gestation displayed the normal posture of female urination (arched the back and slightly crouched hind legs) (Clarke et al., 1976). An interesting assessment of these findings presented by Katz (1987), stated that these differences may be attributed to the relative contributions of the differentiation of

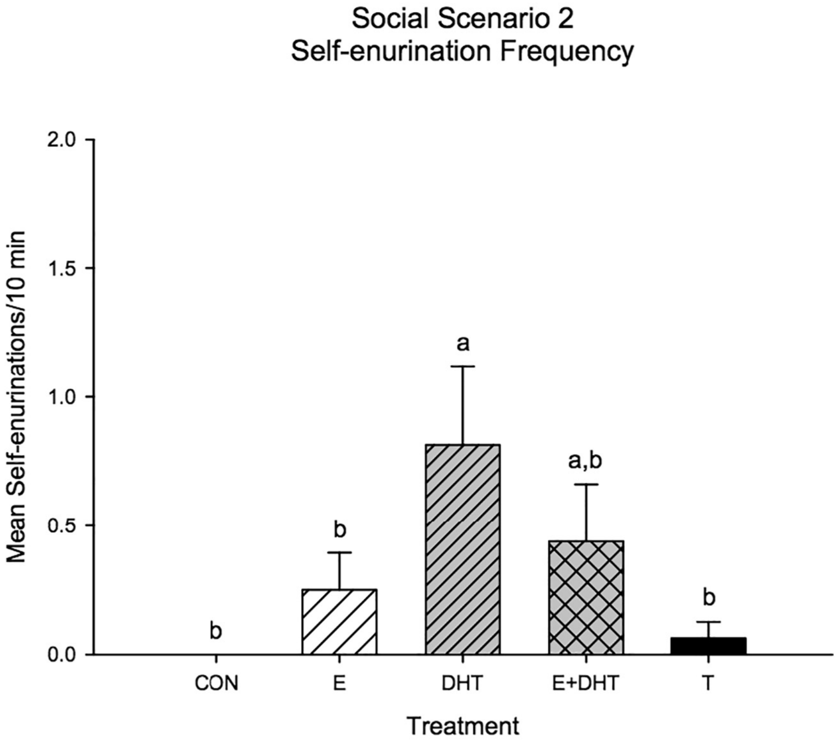

Fig. 5. Opportunity to court and breed estrous does negatively affects self-enurination frequency in androgen-treated wethers: Self-enurination frequency (Mean ± SEM) displayed by the wethers treated with CON (vehicle control), T (testosterone propionate), E + DHT (estradiol benzoate + dihydrotestosterone propionate), E (estradiol benzoate), and DHT (dihydrotestosterone propionate) during a 10-min test. In social scenario 2, wethers interacted freely with estrous does. For each treatment n = 8. Bars with different superscripts differ ($P < 0.05$).

peripheral structures and the differentiation of the central nervous system. Early in development, differentiation of peripheral structures would account for the pulsatile release of urine by the development of urethral musculature caused by androgen stimulation, while differentiation of the central nervous system at this time would be more likely to account for the urinary posture, which is likely a result of behavioral masculinization (Katz, 1987). Thus, it is plausible that androgens influence both the peripheral structures and the central nervous system early in development to enable the behavior to present itself. This would account for the observation of an occasional SE in untreated wethers, as displayed by a CON-treated wether in social scenario 1 (Fig. 3).

Further evidence presented in other species show that androgens, particularly DHT, which binds with a high affinity to androgen receptors, act on the central nervous system to influence behaviors. For example, in rats Hart (1968) and Breedlove and Arnold (1980) found

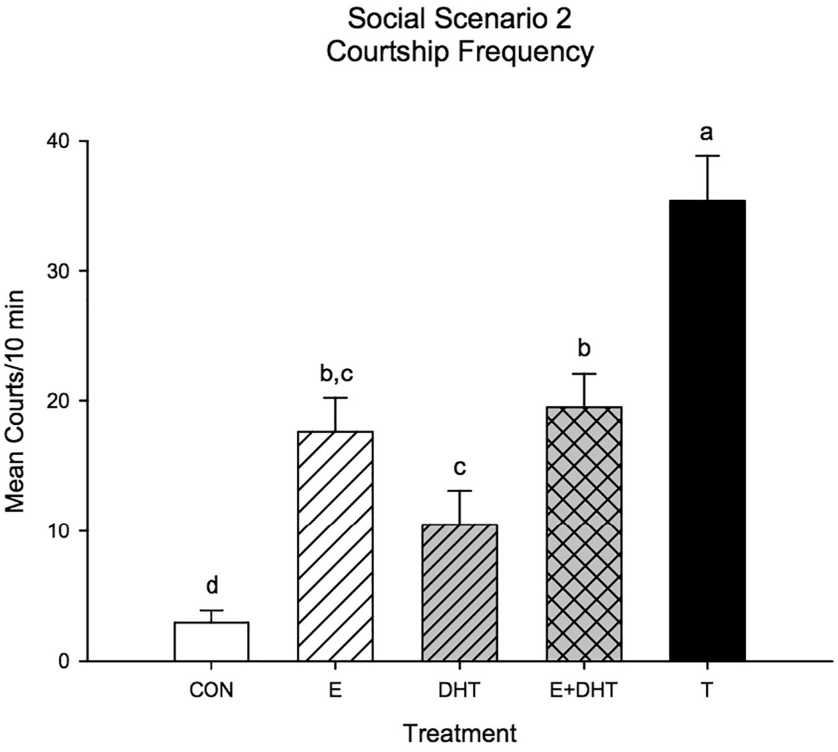

Fig. 6. Both hormone treatment and socio-sexual conditions affect courtship: Courtship frequency (Mean ± SEM) displayed by the wethers treated with CON (vehicle control), T (testosterone propionate), E + DHT (estradiol benzoate + dihydrotestosterone propionate), E (estradiol benzoate), and DHT (dihydrotestosterone propionate) during a 10-min test. In social scenario 2, wethers interacted freely with estrous does. For each treatment n = 8. Bars with different superscripts differ ($P < 0.05$).

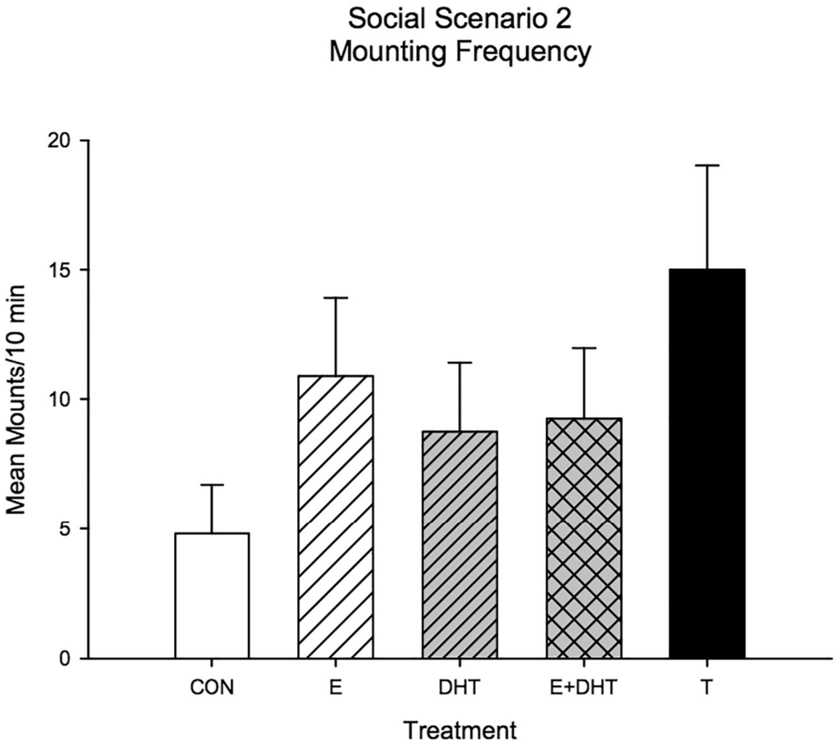

Fig. 7. Hormone treatments do not affect mounting frequency: Mount frequency (Mean ± SEM) displayed by the wethers treated with CON (vehicle control), T (testosterone propionate), E + DHT (estradiol benzoate + dihydrotestosterone propionate), E (estradiol benzoate), and DHT (dihydrotestosterone propionate) during a 10-min test. In social scenario 2, wethers interacted freely with estrous does. For each treatment n = 8.

accumulations of androgens and their metabolites in regions of the spinal cord associated with erection and ejaculation reflexes. Current understandings are that penile erections are caused by creating a change in the activity of efferent autonomic pathways to erectile tissues from the spine (Giuliano and Rampin, 2000). These spinal neurons are activated by peripheral and supraspinal cascades originating from genital sensory information, receptors in the spinal cord, brainstem and hypothalamic nuclei (Giuliano and Rampin, 2000). In the dorsolateral nucleus of the male rat, motoneurons innervating the external urethral sphincter that function in micturition are intermixed with those innervating the ischiocavernosus, which are involved with penile erections (McKenna and Nadelhaft, 1986). In light of this information, our finding that SE is androgen-dependent could suggest that SE is a behavior displayed in response to an erection occurring with the inability to engage in copulation, but this idea needs further study.

The testicular feminization mutation model in rodents has indicated that androgen receptors are normally involved in the masculinization of many sexually dimorphic brain regions, influencing a variety of

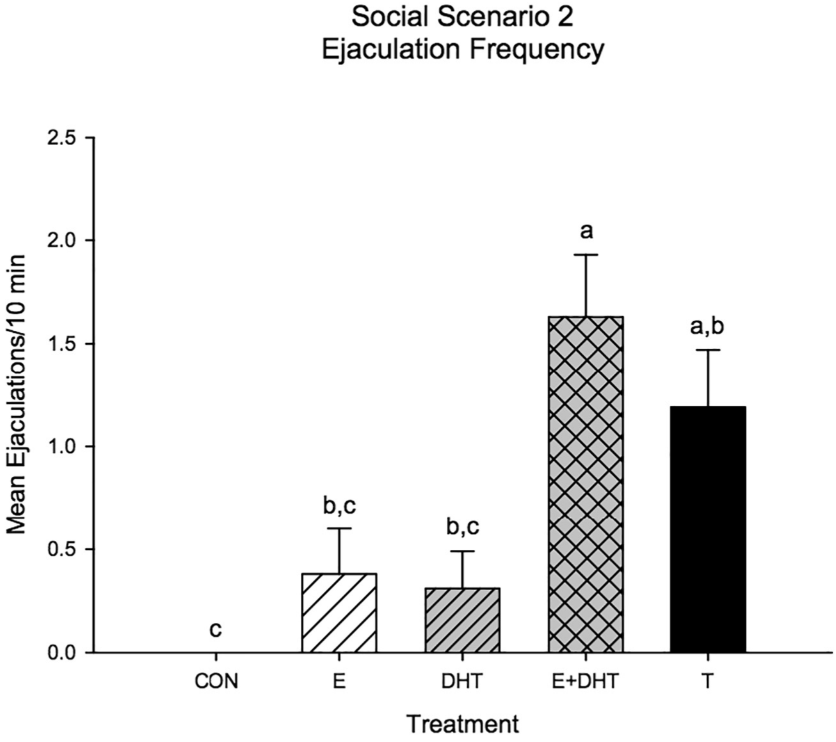

Fig. 8. Hormone concentrations do not affect frequency of ejaculation: Ejaculation frequency (Mean ± SEM) displayed by the wethers treated with CON (vehicle control), T (testosterone propionate), E + DHT (estradiol benzoate + dihydrotestosterone propionate), E (estradiol benzoate), and DHT (dihydrotestosterone propionate) during a 10-min test. In social scenario 2, wethers interacted freely with estrous does. For each treatment n = 8. Bars with different superscripts differ ($P < 0.05$).

behaviors including sexual behaviors, stress response and cognitive processing (Zuloaga et al., 2008). These findings support the hypothesis that androgens influence brain masculinization via binding to androgen receptors resulting in the display of male-like sexual behaviors. Perhaps it is not estrogen, aromatized from testosterone, but androgen itself that drives the masculinization of brain structures associated with the display of SE. More recent work by Juntti et al. (2010) suggests that androgen receptor activation is only responsible for the execution of sexual behaviors and not the programming necessary for these behaviors in mice. These findings are consistent with the finding in this study that nonaromatizable androgens cause an increase in the probability of SE later in life. However, they raise further questions on how sex hormones may influence the masculinization of brain structures in utero, during early development, and during puberty to affect this behavior in adulthood.

The frequency of the male goat's sexual behaviors is influenced by his environment. The overall frequency of courtship in groups that courted (T, E, E + DHT) in social scenarios 1A and 1B was greater than the same groups in social scenario 2 (Figs. 4, 6). To explain this difference, courting bucks in social scenario 1A and 1B were observed courting more heavily at the onset of the test period and appeared to lose interest in the stimulus over time. This was likely due to learned helplessness caused by distance and containment. In social scenario 2, courting bucks' courtship frequency was limited only by their own motivation.

Wethers in scenario 1A and 1B that self-enurinated (T, DHT, E + DHT), did so more frequently than the same groups in scenario 2 (Figs. 3, 5). This difference is explained by the context in which SE occurs. In preliminary studies directed at finding scenarios that increased the likelihood of SE, it was observed that SE does not usually occur when the buck is tending a female. Instead, SE tends to occur when he is sexually aroused, but not able to court directly and copulate with an estrous female. Examples of this include a buck courting an estrous female through a barrier, or during the post-ejaculatory refractory period. It was observed that in social scenario 2, wethers that courted and self-enurinated in scenarios 1A and 1B (T, E + DHT), chose to spend time engaged in courtship and copulation and only self-enurinated occasionally following an ejaculation (Fig. 3). In scenario 2, DHT-treated wethers rarely courted the estrous females, subsequently increasing the likelihood for an SE to occur (Figs. 5, 6). These findings support the hypothesis that self-enurination appears to occur during periods of sexual frustration; in this case, the inability of bucks to court and copulate with estrous does with which they had visual and auditory contact. When physical contact, direct courtship, and copulation can occur, the likelihood of SE decreased. In light of these findings, it appears that SE is not part of the buck's courtship display but has an alternative significance.

Relative contributions of social context and endocrine milieu to the activation of sexual behaviors were teased apart in this experiment. While the likelihood of the male to display courtship behaviors or SE is dependent on the presence of androgens and/or estrogens acting either prenatally (organization) or during adulthood (activation), the social context plays a critical role. For the goat the susceptibility to contextual influence appears to be specific behavior-dependent. For example, wethers would not SE when they were able to court and mount an estrous doe freely, even though the same hormone treatment activated the behavior in other sexually relevant contexts, i.e. limited direct contact with females (Fig. 5). In contrast, mounting occurred regardless of steroid treatment, including none, if the context allowed, i.e., estrous female present (Fig. 7). These males were exposed to androgens prenatally and postnatally before castration was performed, so the brain was masculinized to some extent. These findings suggest that both context and endocrine profiles affect the likelihood of a buck to display SE and other sexual behaviors. It is likely that contextual clues modify which behaviors are more likely to be expressed.

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