



Estrous female goats use testosterone-dependent cues to assess mates

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ABSTRACT

In a promiscuous species like the domestic goat (*Capra hircus*), in which maternal investment is greater than paternal investment, a female may mate selectively with a more-fit male to improve her reproductive fitness. Testosterone (T) controls a large suite of male-typical behaviors and morphological characteristics. High T concentrations may be energetically costly or even detrimental to survival; thus, preventing lower quality males from falsely advertising their fitness. Three preference studies were conducted to examine if females use T-dependent cues to assess potential mates. For Experiment 1, females were given a choice between a pair of morphologically similar males, bucks (intact males) and stags (post-pubertally castrated males), during the breeding and non-breeding seasons. In both seasons, females preferred the bucks compared to stags. In Experiment 2, females were given a choice between bucks, stags and wethers (pre-pubertally castrated males) during the non-breeding season. For some comparisons, castrated males received 25 mg testosterone propionate (TP) or were untreated. Females preferred TP-treated males compared to untreated males and showed no preference when given a choice between either two TP-treated or two untreated males. In Experiment 3, females were given a choice between a pair of bucks and a pair of stags treated with 25 mg TP during monthly tests in the breeding season. At each monthly test, females preferred the males with higher T concentrations near the time of the behavior test. These studies suggest that females use T-dependent cues to assess potential mates, and T concentrations may indicate a male's overall fitness.

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Introduction

Female mate choice is the ability of a female to distinguish among, and mate selectively with, specific phenotypes (Krebs and Davies, 1978). Sexual selection theories suggest that for promiscuous species in which males and females breed with several partners and there is no paternal care, females often breed with higher quality mates. Males, on the other hand, will attempt to breed with a large number of partners (Trivers, 1972). The ability of the female to distinguish among high and low quality males is of critical importance and is a major determinant of her reproductive fitness. Extravagant secondary sexual characteristics such as bright coloration, intricate songs, ornate visual signals and chemical cues have all received considerable attention in the study of sexual selection, as females often choose to mate with individuals displaying such characteristics (Andersson, 1982; Gentner and Hulse, 2000; Gosling and Roberts, 2001; Waitt, et al., 2003). Although extravagant characteristics may predispose males to predation, these cues may serve as an honest indicator of a male's fitness and increase his access to potential mates (Darwin, 1871). Females that choose individuals displaying extravagant

characteristics will increase the likelihood that their male offspring will also be preferred, thus, increasing the female's reproductive fitness.

For many species, testosterone (T) regulates the expression of a large suite of male secondary sexual characteristics (reviewed in: Hau, 2007; Rhen and Crews, 2002). High T concentrations may impose a cost to the male as they have been shown to negatively affect a male's health by causing immune suppression (Grossman, 1984; Marsh and Scanes, 1994; Mougeot, et al., 2004; Peters, 2000). Duckworth et al. (2001) and Folstad and Karter (1992) argue that T-dependent cues are plastic and dependent upon health condition, specifically parasite load. Accordingly, males with higher parasite loads display a lower expression of secondary sexual characteristics than males with lower parasite loads. High T concentrations have also been shown to be energetically costly for a male to maintain, causing increased metabolic rate (Buchanan, et al., 2001) and an increase in the loss of fat reserves (Ketterson, et al., 1991; Wingfield, 1984). Further, males expressing male-typical reproductive behaviors such as territory marking and defense, mate guarding and courtship are unable to simultaneously forage or hunt for food (Gaunt, et al., 1996; Marler and Moore, 1989), likely leading to decreased body weights. Males with limited access to food or in poor health would not be able to display and/or maintain a high expression of secondary sexual characteristics (Zahavi, 1975). In effect, T production and resulting T-dependent characteristics may be an honest indicator of a male's potential fitness.

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Altogether, males that have higher circulating T concentrations are more likely to be preferred by females than males with lower T concentrations.

In the majority of seasonally-breeding species, males show a circannual increase and decrease in circulating T concentrations. Testosterone concentrations increase and reach maximal concentrations early in the breeding season and decrease thereafter, becoming minimal in the non-breeding season (Busso, et al., 2005; Delgado, et al., 2004). During the breeding season, high serum T concentrations permit the expression of secondary sexual characteristics. In the non-breeding season, there is a decrease in size and activity of the testes (Goritz, et al., 2006; Minter and DeLiberto, 2008; Ritters, et al., 2000) and an associated decrease in the production of reproductive hormones, specifically T. Further, there is a deficit in male-typical reproductive behaviors and secondary sexual characteristics. Castration prior to puberty, often results in males displaying a deficit of T-dependent characteristics. Males castrated post-pubertally show a decrease in reproductive behaviors, sometimes taking upwards of 12 months before there is a complete loss in reproductive behavior (Costantini, et al., 2007; D'Occhio and Brooks, 1980; Davidson, 1966; Hart and Jones, 1975). Testosterone replacement can restore these characteristics similar to the level of an intact male during the breeding season (Beach, 1949; D'Occhio and Brooks, 1980; Foote, et al., 1977; McGinnis, et al., 1989).

In addition, females may also use male morphology, as a means of distinguishing between sexually mature and immature males. Morphological characteristics such as the development of fatty cheek pads in orangutans (Winkler, 1989), darkening of the mane in lions (West and Packer, 2002), the number of feathers in the peacock's train (Manning, 1989), and body size of elephant seals (Haley, et al., 1994), are all examples of age-dependent morphological characteristics that females may use to distinguish between sexually mature and immature males. In a variety of species, including beetles (Conner, 1989), goats (Cote and Hunte, 1993), black-billed magpies (Komers and Dhindsa, 1989), African elephants (Poole, 1989), and crickets (Zuk, 1988), females have shown a preference for older males as mates. One justification for this preference is that age, rather than T concentrations may be an honest indicator of genetic quality, and good genes may account for the increased survivability of older males (Kokko and Lindström, 1996). In mating with older males, females stand to benefit from these good genes by passing them on to their offspring.

The goat is an excellent model for the study of female mate choice. In the wild, goats are promiscuous and offspring care is exclusively maternal. Thus, the goat (*Capra hircus*) meets the criteria for a species

that should display mate choice. As a domestic species, the goat can be managed and manipulated for experimentation, allowing for a more thorough understanding of mate choice in a large mammalian species. Male goats undergo seasonal behavioral and physiological changes that may be T-dependent. Use of males castrated pre-pubertally (morphologically immature) or post-pubertally (morphologically mature), provides the ability to separate morphological cues from other T-dependent cues such as behavior or chemical signaling to gain a better understanding of female preference. The objectives of this study were to examine if morphological and/or other T-dependent cues are used by females to assess potential mates.

Materials and methods

Animals

All animals were Alpine goats between the ages of 1.5–9 years which 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. The breeding season for the Alpine goat begins in mid-August and terminates near the end of January in the northern hemisphere. Focal goats were estrous-synchronized females. Goat males used in the preference tests were in various reproductive states. Bucks are gonadally intact males with typical male morphological characteristics including a muscular neck and thick beard. Stags are males castrated post-pubertally and they have morphological characteristics similar to those of a buck. Wethers are males castrated pre-pubertally and they have morphological characteristics similar to those of females (Fig. 1).

Estrus synchronization and detection

Focal goats were estrus-synchronized females drawn from a herd of 24. The herd was divided into two groups which were estrus-synchronized on alternating weeks. Estrus synchronization was accomplished using a sequential treatment of prostaglandin (PGF_{2α}). During the breeding season each female received two injections of 10 mg PGF_{2α} (dinoprost tromethamine, i.m.) at 13 days prior and 51 h prior to the behavior test as modified from Ott et al. (1980). For experiments conducted as females entered the non-breeding season, estrus was either synchronized using the protocol previously discussed or induced by providing exogenous progestins and estradiol from the protocol developed by Billings and Katz (1997; 1999).

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. All females, regardless of estrous state, were tested in the behavior experiment; however, only data from estrous females are reported. Number of estrous females used in each preference test is indicated in Table 1.

Testosterone propionate treatment

Castrated males received 25 mg testosterone propionate (TP) s.c., 3×/week beginning one month prior to the behavior test (TP-treated males are designated as Wether TP or Stag TP). Previous studies by our laboratory have shown that 25 mg is sufficient to activate male reproductive behaviors in wethers (unpublished data). Injections

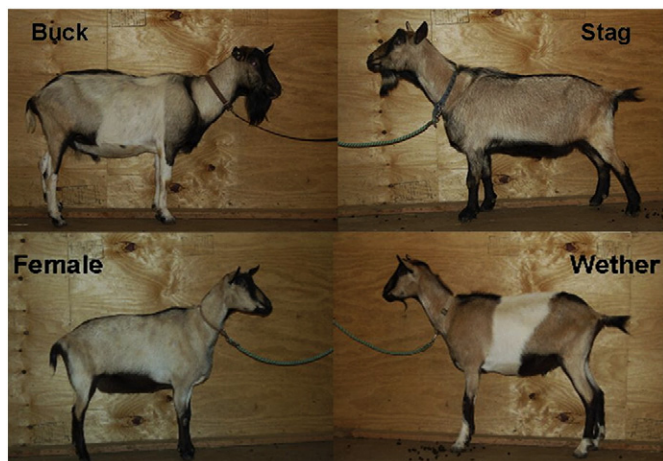


Fig. 1. Goat phenotypes: Note similarities between buck and stag morphology as well as female and wether morphology.

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