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Female goats use courtship display as an honest indicator of male quality

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ABSTRACT

Due to the differential cost of reproduction in promiscuous species, like domesticated goat(s) (*Capra hircus*), it is expected that females should mate with higher quality males, while males should mate with a greater number of females. Females may use conspicuous secondary sexual characteristics of males such as courtship display to distinguish among high and low quality males. Testosterone (T) controls a large suite of secondary sexual characteristics and variation in T concentrations may account of differences in courtship rates. Two studies were conducted to examine the relationship between T concentrations and courtship rate and its role in mammalian female mate choice. Experiment 1 utilized bucks (intact males) and Experiment 2 utilized T-replaced wethers (castrated pre-pubertally). During the first year of Experiment 2, T-replaced wethers received either vehicle control (CON), 25 mg or 100 mg testosterone propionate (TP). During the second year of Experiment 2, T-replaced wethers were treated with either 5 mg, 15 mg or 25 mg TP. For all experiments, mean courtship rates and circulating T concentrations were measured, as well as female preference for males displaying different courtship frequencies. T concentrations and courtship rate were positively correlated for bucks and estrous females preferred high courting bucks. Males receiving 25 mg and 100 mg TP courted females at a similar rate, but both were significantly higher than courtship rates of the CON wethers. Courtship rates of the 25 mg, 15 mg and 5 mg TP-treated males were all significantly different. Females did not show a preference between the 100 mg or 25 mg TP-treated wethers, however both were preferred in comparison to the CON wethers. Females did not show preference between the 25 mg or 15 mg TP-treated wethers, however both were preferred in comparison to the 5 mg TP-treated wethers. Taken together, these studies suggest that courtship rate is T-dependent. Further, females can use courtship rate to distinguish among males.

Introduction

Conspicuous secondary sexual characteristics such as bright coloration, scent marking, and courtship cues have all received considerable attention in the study of sexual selection (Andersson, 1994). Trivers (1972) proposed that for species in which there is greater maternal investment compared to paternal investment, females should breed with higher quality males while males should breed with a greater number of females. In this context, conspicuous secondary sexual characteristics may not be arbitrary, but rather serve as an indicator of a males' potential reproductive fitness (Malo et al., 2005; Sheldon, 1994). According to Zahavi's (1975, 1997) handicap principle, the cost of the characteristic should be directly related to the reliability of the indicator or cue. Consequently, secondary sexual characteristics serve as an honest indicator of the male's quality with high quality males displaying more conspicuous secondary sexual characteristics than those who are lower quality (reviewed in: Andersson, 1994). Females who mate with highly fit individuals should benefit directly by increasing their reproductive fitness, assuming their offspring inherit the desired trait(s) for their sires. Thus, secondary sexual characteristics may play an important role in a female's mate preference.

Male courtship is often accompanied by visual ornamentation such as that seen by the classic examples of the in feathers of a male peacock (Petrie et al., 1991) or swallow (Møller, 1988), or intense coloration such as that displayed by stickleback fish (Bakker, 1993) or large antler length as that displayed by male roe deer (Vanpé et al., 2010). Courtship may also be accompanied by vocalizations such as roars of red deer (Charlton et al., 2007; McComb, 1991), bellows of bison (Wyman et al., 2008) and courtship vocalizations by the satin bowerbird (Loffredo and Borgia, 1986) and marginated tortoises (Sacchi et al., 2003). Both visual and auditory cues may aid in female mate choice by further exaggerating courtship cues displayed by the male (McLintock and Uetz, 1996). However, for this paper, we will focus on courtship display only and in this context we define courtship as male repetitive behaviors which occur toward the female prior to mating.

If females use courtship cues to distinguish among high and low quality males, then sexual selection pressures should give rise to variation in the intensity or rate of display of male courtship. Male courtship rate and frequency of courtship display are sexually selected characteristics that have been well studied in birds (Jiguet and

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Bretagnolle, 2001; Patricelli et al., 2002), fish (Knapp and Kovach, 1991; Vinnedge and Verrell, 1998), and amphibians (Karino, 1995), with higher performing males being preferred by females. One explanation for this preference for higher performing males is that such displays may provide information to the female about the male's quality, and thus, her potential fitness gains. Studies using several avian species suggest that male courtship display may be an honest indicator of a male's age (Loffredo and Borgia, 1986), experience (Yasukawa, 1981), and/or body condition (Genevois and Bretagnolle, 1994; Simmons, 1988). Male courtship may provide evidence of a male's quality as demonstrated by studies on reptiles (Galeotti et al., 2005) and birds (Hamilton and Zuk, 1982; Hardouin et al., 2009; Jiguet and Bretagnolle, 2001; Martín-Vivaldi et al., 1999). Further, courtship may provide information about a male's parental ability as displayed by birds (Buchanan and Catchpole, 2000) and fish (Knapp and Kovach, 1991; Takahashi and Kohda, 2004).

Testosterone (T) often plays a key role in regulating male-typical reproductive behaviors including courtship behavior (reviewed in: Hau, 2007; Rhen and Crews, 2002). High T circulating concentrations impose energetic costs (Buchanan et al., 2001; Wingfield et al., 2001) and immune suppression (Decristophoris et al., 2007; Marsh, 1992; Marsh and Scanes, 1994) to male vertebrates; preventing a male from falsely advertising his status. Testosterone concentrations may be an honest indicator of a male's fitness and resulting T-dependent behaviors such as courtship may be used as a cue to assess fitness. Accordingly, a relationship between male quality and T concentrations should exist as high quality males could invest more into courtship display to gain access to mates while low quality males invest more into survival (Duckworth et al., 2001; Folstad and Karter, 1992; West and Packer, 2002). Testosterone replacement studies using birds (Mougeot et al., 2004; Takahashi and Kohda, 2004) have provided unique opportunities to investigate the relationship between testosterone concentrations, courtship, immunosuppression, and body condition, providing inference and comparisons to wild populations.

Little is known about courtship and its role in mammalian female mate choice; however we do know that courtship displays are common in the majority of ungulate species (reviewed in: Walther, 1984) and are often displayed exclusively during the breeding season. The domesticated male goat also displays courtship behaviors during the breeding season including a foreleg kick, head-twist and nudge, and tongue flick. Upon encountering a female, a male will generally first display a foreleg kick whereby the male locks his front legs and strikes the female with his hoofs or foreleg. If the female does not run away, the male may follow the foreleg kick with a head-twist and nudge, and tongue flick, which are done simultaneously. Display of the tongue flick results in a gobble sound. The male will repeat these behaviors until he mounts the female. Further, as one of the oldest domesticated species, it would be expected that females should not display mate choice. However, previous studies in our lab have shown that females can distinguish among morphologically similar males and show preference for males with higher T concentrations (Longpre and Katz, 2011), suggesting that the underlying mechanism of mate choice are robust as artificial selection pressures have not reduced the strength of sexual selection within the species. If variation exists among male courtship rates, which are correlated with T concentrations, and females' show preference for males that display a higher rate of courtship, then these studies suggest that the goat is an excellent model for the study of courtship behavior, testosterone concentrations, honesty and female mate choice. To examine courtship and female mate choice, two experiments were designed with Experiment 1 using gonadally-intact males (bucks) and Experiment 2 using pre-pubertally castrated males (wethers) supplemented with testosterone. The objectives of both experiments were twofold. The first objective was to examine the correlation between courtship rate and T concentrations. The second objective was to test if females are able to distinguish among males that court females at different rates. It was predicted that male courtship behavior is T-dependent and females prefer high courting males.

Materials and methods

Animals

All animals were Alpine goats between the ages of 1.5–9 years and received a diet consisting of grass hay and grain, as well as 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. Number of males used for courtship rate test and as goal animals for the preference tests varied and were in various reproductive states as described in the methods sections for each experiment. In addition, all males used were disbudded shortly after birth, resulting in no horn growth.

Estrous synchronization and detection

Focal goats were estrous-synchronized females drawn from a herd of 24. The herd was divided into two groups which were estrus-synchronized on alternating weeks. Estrous synchronization was accomplished using a sequential treatment of prostaglandin ($PGF_{2\alpha}$). During the breeding season, each female received two injections of 10 mg $PGF_{2\alpha}$ (dinoprost tromethamine, i.m.) at 11 to 14 days prior and 51 h prior to the behavior test as modified from Ott et al. (1980). For experiments conducted using ovariectomized (OVX) females, estrus was induced by providing exogenous progestins and estradiol (Billings and Katz, 1997, 1999).

Standing estrus was detected prior to each preference 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.

Blood sampling and radioimmunoassay (RIA)

Blood samples were collected via jugular venipuncture. For Experiment 1, blood samples were collected from bucks on a weekly basis (September through December) at 0800. For Experiment 2, blood samples were collected once from the TP-treated males over a 48-hour time period at the following time points relative to the injection of TP: 0, 0.25, 0.5, 1, 2, 6, 12, 24, and 48 h. Serum was stored at −20 °C until assayed.

Serum testosterone concentrations were determined by commercial RIA kit validated in our laboratory for goat serum (bucks: Beckman Coulter DSL-4000, Webster, TX; TP-treated wethers: Siemens Healthcare Diagnostics, Inc., Coat-A-Count Total Testosterone, Los Angeles, CA). The minimum detection limit of the DSL-4000 assay was 0.02 ng/ml and the inter-assay coefficient of variation was 12%. For Experiment 2A, the minimum detection limit of the Coat-A-Count Total Testosterone assay was 0.002 ng/ml and the inter-assay coefficient of variation was 9%. For Experiment 2B, the minimum detection limit of the Coat-A-Count Total Testosterone assay was 0.01 ng/ml and the inter-assay coefficient of variation was 3%.