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While males fight, females choose: male phenotypic quality informs female mate choice in mammals

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Theoretical support exists for an exaggerated male structure to serve as both a weapon for intrasexual competition and as an ornament to signal quality and promote female choice. However, there is little, if any, evidence to support this theory in male–male competition breeding systems. Using white-tailed deer, *Odocoileus virginianus*, as a model species, we manipulated antler size on males while controlling for body size and age and allowed 25 oestrous females the opportunity to choose between pairs of segregated males with either large or small antlers. By segregating males, we were able to remove any intrasexual male competition and isolate the effects of female choice. Using various behavioural indications of female choice, we demonstrate that females prefer males with large antlers to those with small antlers. Because antler size is heritable in deer, this female preference for larger antlers may be adaptive by increasing the reproductive success of her male offspring. Our unique antler manipulation study supports the armament-ornament model where male weapons can simultaneously serve as ornaments to females and weapons in male–male competition breeding systems.

Darwin's (1871) theory of sexual selection included two principal mechanisms: intrasexual competition (usually between males) for breeding access, and mate choice (usually by the female) based on desirable traits in the opposite sex. His theory proposed that male secondary sexual characteristics evolved from sexual selection, but the specific mechanism (competition or mate choice) has been debated across taxa (red-winged blackbirds, *Agelaius phoeniceus*: Peek, 1972; pied flycatchers, *Ficedula hypoleuca*: Järvi, Røskaft, Bakken, & Zumsteg, 1987; bighorn sheep, *Ovis Canadensis*: Hogg, 1987; reindeer, *Rangifer tarandus*: Prichard, Finstad, & Shain, 1999; white-tailed deer, *Odocoileus virginianus*: Ditchkoff, Lochmiller, Masters, Hoofer, & Van Den Bussche, 2001; lions, *Panthera leo*: West & Packer, 2002; red deer, *Cervus elaphus*: Mysterud, Meisingset, Langvatn, Yoccoz, & Stenseth, 2005; roe deer, *Capreolus capreolus*:Vanpé et al., 2007). It is well accepted that many female birds select mates based on secondary sexual traits that signal their genetic quality (Andersson, 1982; Clutton-Brock & McAuliffe, 2009; Møller et al., 1998; Pryke, Andersson, & Lawes, 2001). Some male fiddler crabs, *Uca* pugilator, grow a gigantic claw (Salmon, Hyatt, McCarthy, & Costlow, 1978) and some male pheasants grow long spurs (von Schantz et al., 1989), both of which have dual utility as a weapon and an ornament (Berglund, Bisazza, & Pilastro, 1996). In mammals, however, it can be difficult to determine whether the weapon also signals quality to the female, simultaneously serving as an ornament.

Secondary sexual traits in mammals, such as body mass and size of weapons, may provide an advantage in male intrasexual competition for access to mates while simultaneously functioning as indicators of male genetic quality or status (Barette & Vandal, 1986; Berglund et al., 1996; Clutton-Brock, 1982; Ditchkoff et al., 2001; Geist, 1971; Pelletier & Festa-Bianchet, 2006; Vanpé et al., 2007). Berglund et al. (1996) provided evidence that weapons (armaments for male–male competition) can be used as ornaments to advertise genetic quality or status to females. However, the coercion avoidance hypothesis predicts that females should avoid using weapons as a criterion for male quality because males can use the weapon to coerce breeding. Instead, a female should use an ornament that is not linked to the male's ability to coerce breeding (Pradhan & Van Schaik, 2009). Dual purposes for male secondary sexual traits make it difficult to disentangle female mate choice from male intrasexual competition and coercive tactics (Clutton-Brock, Deutsch, & Nefdt, 1993). Thus, to properly evaluate female

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mate choice, experiments must control for male intrasexual competition (Charlton, 2013).

The ability to isolate individual male traits from other aspects of the male phenotype is challenging and limits detection of the influential sexual traits that females are selecting (Charlton, 2013). Additionally, controlled experiments are required to determine which of several allometrically related male traits females are selecting. For example, antler size in deer is a function of age and body size, which are associated with reproductive success (Barette & Vandal, 1986; Clutton-Brock, 1982; Jones, Strickland, Demarais, & DeYoung, 2011; Mysterud et al., 2005; Newbolt et al., 2017). Manipulation of antler size while controlling for age and body size is required to determine which trait influences female choice (Clutton-Brock & McAuliffe, 2009), but previous attempts to manipulate antler size have failed to show any effects (Lincoln, 1994; McComb & Clutton-Brock, 1994).

We hypothesized that antlers serve as an ornament that influences female choice. If true, our study would provide evidence for the signalling function of antlers adding to what we already know of their use in combat, consistent with the armament-ornament model proposed by Berglund et al. (1996). Using white-tailed deer, we tested the ornament function of antlers by manipulating antler size and controlling for allometrically related traits, like body size, to isolate the influence of a single secondary sexual characteristic on female mating choice.

METHODS

Site Description

White-tailed deer used in this study were wild-caught deer or offspring of deer captured from 29 sites throughout Mississippi (Michel, Demarais, Strickland, & Belant, 2015). Deer were maintained at the Mississippi State University Rusty Dawkins Memorial Deer Unit (MSU Deer Unit). The MSU Deer Unit, Oktibbeha County, Mississippi, U.S.A., is subdivided into 5 0.4–0.8 ha housing pens and 6 0.05–0.07 ha holding pens. Each housing pen contained water and two feeders with 20% crude protein deer pellets (Cargill Sportsman's Choice Record Rack, Cargill, Inc., Minneapolis, MN, U.S.A.) supplied ad libitum. Each holding pen contained water and one feeder. Available forages within pens included white clover (*Trifolium repens*) and various grasses and forbs.

The trial pens used in this study consisted of three holding pens located side by side and furthest from the housing pens. We installed video cameras in the centre pen facing down each fence line shared with the outer pens. The video cameras are capable of both day and night recording using infrared. We installed infrared illuminators to improve night-time video footage. We removed shade cloth from shared fence lines so that each animal could easily see an animal housed in an adjacent pen. We placed the food and water in the centre of the middle pen and on the outside fence of the outer pens (Fig. 1).

Oestrus Induction

Females in oestrus would be most likely to exhibit an active choice (Charlton, Reby, & McComb, 2007), so we induced the oestrus of adult females using intravaginal controlled internal drug-release dispensers (CIDR®, Eazi-Breed; Zoetis Animal Health, Florham Park, NJ, U.S.A.) containing progesterone released at a controlled rate (Wheaton, Carlson, Windels, & Johnston, 1993). We removed CIDRs after 14 days (Ainsworth & Downey, 1986; Rhodes & Nathanielsz, 1988). The majority (~80%) of females enter oestrus 24 h after removal of oestrus-inducing CIDR devices (Rhodes & Nathanielsz, 1988). We induced oestrus in one doe every 2 days from mid-November until mid-March so that each female's preference was expressed without influence of other females; that is, they were independent samples.

Sedation Procedure

We used a Pneu-Dart projection system (Pneu-Dart, Inc., Williamsport, PA, U.S.A.) with telazol (4.4 mg/kg) and xylazine (2.2 mg/kg) or with BAM™ (0.55 mg/kg butorphanol tartrate (27.3 mg/ml, Zoo- Pharm, Laramie, WY, U.S.A.) + 0.18 mg/kg azaperone tartrate (9.1 mg/ml, ZooPharm) + 0.22 mg/kg medetomidine HCl (10.9 mg/ml, Zoo-Pharm)) to sedate females for CIDR insertion and removal. We administered tolazoline (4.0 mg/kg; Miller et al., 2004) to reverse effects of xylazine or naltrexone HCl (25 mg (50 mg/ml, ZooPharm)) and atipamezole (100 mg (25 mg/ml, ZooPharm)) to reverse effects of BAM™.

Trials

To evaluate mate preference, we placed each female ($N = 25$) into the trial holding pen for 36 h immediately after CIDR removal to increase the likelihood that she would be in oestrus while expressing her preference (Rhodes & Nathanielsz, 1988). This proved a correct assumption because every female stood for breeding within 12 h of release into a separate breeding pen (D. Morina, personal observation).

On each of two sides of the trial holding pen was a similar holding pen containing a male with an antler manipulation treatment (Fig. 1). Two sets of males, a pair of 6-year-olds and a pair of 1-year-olds, were used in the trials. Two sets of large antlers and two sets of small antlers were also used in the trials. Antler size was measured using the Boone & Crocket scoring system (Nesbitt, Wright, Buckner, Byers, & Reneau, 2009) converting measurements to metric units and without accounting for deductions. Each pair of males was the same age and similar body mass (6-year-old set = 1.3% difference, 1-year-old set = 8.0% difference). We installed the first set of large antlers (first set = 403 cm, second set = 425 cm) on one member of the pair and the first set of small antlers (first set = 152.5 cm, second set = 170.7 cm) on the other (Fig. 2). Antler size of deer harvested in Mississippi between 1991 and 2002 averaged 211.8 cm and ranged from a minimum of 25.4 to a maximum of 475.2 cm ($N = 128\,707$; SD = 32.1; Strickland, 2016). Therefore, the antler sizes we assigned as large and small are within the naturally occurring size range. The antler manipulation process required anaesthetization, so we allowed 24 h for the effects of the drugs to subside before starting any choice trials. After the first several trials, we rotated the males between the two holding pens adjacent to the trial holding pen to control for potential bias due to pen location. After several more trials, we exchanged antler manipulation treatments within the pair to control for individual animal bias while also using the second set of large and small antlers to control for potential bias due to preference for a particular set of antlers. By doing so, each male was presented as a ‘candidate’ with different sets of large and small antlers over the course of the trials. After completing this series of trials using one pair of 6-year-old males, we repeated the process with one pair of 1-year-old males. All animal handling procedures followed methods approved by the Mississippi State University Institutional Animal Care and Use Committee protocol number 15-074.

We conducted trials using 25 female deer in oestrus. The pair of 6-year-old males was the basis for choice by 20 females, seven with them in one pen assignment, seven with them in opposite pen assignments, and six with a different set of large and small antlers. Trials using the pair of yearling males were ended after five trials in one set of pens due to an injury to one of the males.