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To cite this version:

Cécile Vanpé. Male mating systems and sexual selection in ungulates.. Swedish University of Agricultural Sciences. 2005. hal-02833346

HAL Id: hal-02833346
https://hal.inrae.fr/hal-02833346v1

Submitted on 23 Nov 2023

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Introductory Research Essay No 19
Department of Conservation Biology
SLU Uppsala 2005

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Abstract

Strong reciprocal relationships have long been suspected between mating systems and sexual selection, and so different angles of discussion can be pursued to investigate these relationships. In this essay, mating systems are regarded as one of the factors that may influence the strength and consequences of sexual selection.

The ungulates show a wide variety of mating systems, and though most ungulate species are polygynous, male mating tactics range from non-territorial males courting individual estrous females, to both female-defense harem systems and resource-defense territorial systems, and to leks. It is thus interesting to focus on this group to investigate the scope for development of sexual selection in relation to various mating tactics. Based on behavioural ecology and sexual selection theories, it is possible to propose several predictions concerning mechanisms of competition over mates and sexually selected traits favoured by each ungulate mating tactic. The aim of this essay is to review the main sexually selected traits reported in ungulate studies, with special reference to the Cervidae, the Bovidae and the Antilocapridae, and to discuss the fit of them with the theoretical predictions.

Contents

Introduction

Mating systems are defined by the reproductive strategies adopted by individuals of both sexes in order to mate (Clutton-Brock 1989). The ultimate aim of these behaviors can be viewed as the maximization of the relative genetic contribution to subsequent generations. According to general theories of the behavioral ecology, optimal mating strategies tend to be different for the two sexes, because of the size difference between male and female gametes: females produce few large macrogametes rich in energy, whereas males produce a lot of small, highly mobile microgametes (Trivers 1972). According to Trivers (1972), this difference in the size of the gametes can be expressed as a difference in parental investment between the sexes. Females usually allocate more energy in parental investment (including investment in the production of gametes, in the nourishing of the embryo and in the care of offspring) than males. The consequence of this difference in parental investment between the sexes is that males can make many more gametes than females and have the capacity to fertilize a number of females and father a number of young. They should thus attempt to mate with as many fecund females as possible (Trivers 1972). Females, on the other hand, need only one male to be fertilized. Their investment in fewer but larger gametes should make them more careful in their choice of mating partner.

As a consequence, many sexually active males will be searching at a given moment for relatively few receptive females, leading to competition among males for mates, while providing opportunity for females to choose among potential mates. These processes lead to Sexual Selection (Darwin 1871), which concerns variation among individual traits of one sex that affect success in competition over mates and fertilizations. If the differences in the traits are hereditary, sexual selection will lead to the spread of those attributes that enhance reproductive success. The sexual selection of a trait can then be viewed as the differences in reproductive success, caused by competition over mates, and related to the expression of the trait (Andersson 1994).

Darwin (1871) proposed two main mechanisms of mating competition leading to sexual selection of a trait. First, via contest competition (leading to intrasexual selection), which consists of fighting between males to gain access to females. This type of competition over mates creates a selection pressure favoring the development of male traits that enhance their ability to fight and dominate (e.g., increase of body size ; elaboration of organs used as weapons). Second, via mate choice (leading to intersexual selection), which consists of competition between males to attract the females. It leads to the elaboration of structures or behavior patterns that attract females, and that could be reliable indicators of male phenotypic quality. Different signals such as body size, secondary sexual characteristics (e.g., antler size), or behaviors reflecting vigor (e.g., vocalization, display, status) can be used to show male quality. The type of competition over mates favored by sexual selection and the expression of secondary sex traits will differ between the various mating systems. In fact, the mating system can be viewed as one of the main factors that influence the strength and consequences of sexual selection (for a review see Andersson 1994). The purpose of this essay is to investigate the relation between male mating systems and sexual selection in ungulates.

The ungulate group consists of medium sized and large herbivorous mammals. It is classified into five orders: i.e., Artiodactyla (e.g., donkeys, camels, pigs, hippopotamus, peccaries, deer, musk deer, bovids, giraffes), Perissodactyla (e.g., horses, zebras, tapirs, rhinoceroses), and the three primitive orders Hyracoidea, Tubulidentata and Proboscidea (e.g., elephants). The ungulates show a wide variation in morphology, behavior, and social organization among species. The following mating systems have been reported: harem defense, lekking, roving, territoriality (Owen-Smith 1977). It could be thus interesting to focus on ungulates to investigate the differential scope for development of sexual selection in relation to variation in mating systems. I will focus mainly on the case of territoriality, which is very common in ungulates but with a varying incidence among the different families: though territoriality is prevalent among most of the antelope of the subfamily Bovinae, appearing also in some equids, rhinoceros, camelids and antilocaprids, it is generally absent with few exceptions in the wild cattle tribe (Bovini), in sheep and goat (Caprinae), and in deer (Cervidae) (Owen-Smith 1977).

In my essay, I will thus first review the various mating tactics occurring in ungulates in relation to the ecological factors (environmental and sociological) that promote their evolution. I will then expose the potentiality for sexual selection associated with each mating tactic, with special reference to territorial ungulates. Finally, I will give a background to the main sexually selected traits that have been reported in male ungulates, before discussing their fit to our expectations.

1. VARIABILITY OF MALE MATING SYSTEMS IN MAMMALS

a) From monogamy to promiscuity

The ideal way for a male to maximize his reproductive success may be to mate with as many females as possible, leaving the females to provide for all parental care. For a female, the ideal may be to mate and then leave the male to care for the offspring while she accumulates reserves for a future litter (Krebs & Davies 1993). In practice, the apparent conflict of interest in the optimal mating strategies of the two sexes will be resolved according to two factors. First, different species have different physiological and life history constraints which predispose one sex to provide more parental care than the other. Second, ecological factors will influence the costs and benefits associated with parental care and mating tactics (Krebs & Davies 1993). Depending on the parental care constraints, different mating tactics should then be favored.

Although different mating systems have long been recognized in evolutionary biology, there is no strict agreement on their classification (Andersson 1994). The number of mating partners per male and female is one of the main criteria. Monogamy (a male and a female form a pair bond) should be favored mainly when males and females share parental care for the young after birth and in some cases for the eggs. This is the case in the great majority of bird species, but in very few mammals (Krebs & Davies 1993). Polygyny (a male mates with several females, while each female mate with only one male) should be favored particularly when females are strongly predisposed to care for the young (for example because of the prolonged period of gestation and the lactation constraints). This is the case in most mammals, in which males usually provide little parental care after birth, and so females take sole responsibility for the care for the young in order to improve the odds that the offspring will reach reproductive age and transmit the parent’s genes. Two other cases occur, but are more infrequent: polyandry (a female mates with several males, while each male mate with only one female) and promiscuity (both male and female mate several times with different individuals so there is a mixture of polygyny and polyandry). In the first case, it is often the male who provides most parental care, whereas in the second case, either sex may care for the eggs or young (Krebs & Davies 1993).

Among ungulate species, while polygyny is widespread, monogamy (Kleiman 1977) and promiscuity (Preston *et al.* 2003) have been also reported.

b) Male mating tactics among polygynous mammals

In mammals, most species have a polygynous mating system. The reproductive success of females is mainly limited by access to resources necessary to breed and to meet the energy requirements of gestation and lactation (e.g., food, breeding sites), whereas the reproductive success of males is limited more by access to females (Trivers 1972). As a consequence, while the distribution of females should depend primarily on resource dispersion (modified by predation pressure and the costs and benefits of associating with other individuals), males should distribute themselves in relation to female dispersion in order to gain access to as many mates as possible (Krebs & Davies 1993). Clutton-Brock (1989) concludes that the variation in mating behavior of male mammals depends mainly on the defensibility of females, that is directly related to the density and distribution of females, female range size and female group size and stability, and indirectly to the distribution of resources.

Yet males in mammals may have two main options to maximize the number of matings: they could compete for females either directly in male-male contest or indirectly by anticipating how resources will influence female dispersion and competing for resource-rich sites.

The first strategy, named « female defence polygyny » (Elmen & Oring 1977), should be favored when the possibility of finding a receptive female in any one location is low, e.g., at low population densities or when food is unpredictable and females range over large areas. In this case, males gain access to females by following and defending directly one or a group of females against rivals, instead of waiting for the females.

- Where females live in small groups, males can rove and try to associate with individuals in oestrus (Krebs & Davies 1993): this is the « roaming » or « roving » strategy. This mating system is represented among various ungulate species: e.g., white-tailed deer *Odocoileus virginianus* (Hirth 1977), moose *Alces alces* (Whitehead 1972), bighorn sheep *Ovis canadensis* (Hogg 1987), Soay sheep *Ovies aries* (Preston *et al.* 2003), greater kudu *Tragelaphus imberbis* (Owen-Smith 1993).
- Where female groups are larger, the most dominant males may attempt to defend these groups, constituting some « harems » (Krebs & Davies 1993). This is the mating system of red deer *Cervus elaphus* (Clutton-Brock *et al.* 1979, 1982), Burchell's zebra *Equus burchelli* (Klingel 1974), African buffalo *Syncerus caffer* (Sinclair 1974), or reindeer *Rangifer tarandus* (Barrette & Vandal 1990), etc.

The second strategy, named « resource defense polygyny » (Elmen & Oring 1977), should be favored when females are spatially predictable, e.g., when females occupy small ranges containing clumped and high-quality food resources. In this case, males gain access to females indirectly by defending a space against other males and controlling an area with certain vital resources that females require (food, birth sites) and where females can occupy small ranges. This strategy is characterized by « territoriality », which is usually defined in terms of defence, exclusion and site-specific dominance (Owen-Smith 1977). This strategy is particularly common among African antelopes (e.g., impala, *Aepyceros melampus* ; defassa waterbuck, *Kobus defassa*: see Owen-Smith 1977) ; but it also exists in various ungulate family groups: Cervidae (e.g., roe deer *Capreolus capreolus*: Bramley 1970, Sika deer *Cervus nippon*: Miura 1984, Reeves's muntjac *Muntiacus reevesis*: Barrette 1977), Bovidae (e.g., American pronghorn *Antilocarpa americana*: Kitchen 1974), Suidae and Hippopotomidae (see review in Owen-Smith 1977).

Lastly, when neither females nor their home range are defensible, males may aggregate into groups on a communal display area where each male defends a tiny mating territory containing no resources at all and attempts to attract and court females which visit the lek solely for mating (Clutton-Brock 1989, Höglund & Alatalo 1995). Males in this case provide no material resources, only genes. These mating systems are known as « leks » or « male dominance polygyny » (e.g., Grevy's zebra *Equus grevii,* Uganda kob *Kobus kob*, Clutton-Brock 1989 ; fallow deer *Dama dama*, Apollonio 1989).

It should be noted that mating tactics do not only vary between species, but also within species, depending on environmental factors such as population density, habitat, climate, predation pressure (e.g., Lott 1984, Thirgood *et al.* 1999). This seems to be particularly marked for the fallow deer, for which mating systems range from non-territorial males courting individual estrous females (roaming), to both resource-defense polygyny and female-defense harem systems and to leks (Langbein & Thirgood 1989).

2. POTENTIALITY FOR SEXUAL SELECTION IN VARIOUS MATING SYSTEMS

The strength of sexual selection and the type of competition over mates favored by sexual selection will differ between the various mating systems.

a) Influence of mating system on sexual selection strength

Intuitively, it seems likely that the opportunity for sexual selection should increase with party size (Darwin 1871). Previous studies on ungulates (e.g., Jarman 1983) described a continuum of sexual selection intensity with at one extreme, monogamous and monomorphic species, exhibiting similar life-history traits in both sexes, and at the other, highly polygynous and dimorphic species, with differential life-history traits between sexes. In polygynous species, where some males mate with several females and others with none, success in competition over mates is indeed crucial for the fitness of males, the variance in male mating success is usually high and sexual selection is often strong (Andersson 1994). However, although there is little scope for competition leading to sexual selection in monogamous species when each individuals mate with only one other individual during each breeding cycle and when pair bonds are generally stable, sexual selection might also act in these species (e.g., Darwin 1871). Indeed, under strict monogamy, no individual has more than one mate, but some males may have none in the case of skewed sex ratios (Andersson 1994). In addition, mates vary in fecundity or parental ability depending on age, condition, and other aspects. Such differences in quality among mates can lead to sexual selection (Andersson 1994), favoring for example ever-earlier preparedness to breed (Darwin 1871). Lastly, in many species especially in birds, monogamy is not complete, in the sense that some males achieve higher reproductive success through extra-pair copulations (Andersson 1994).

b) Mechanisms of mate competition favored by the various male mating tactics

In lekking, males establish dominance relationships among themselves and female then choose between them, largely on the basis of their status and probably independently of direct material benefits. Sexual selection tends therefore to be inter-sexual and this favors the evolution of some very extreme male epigamic characters and elaborate male behaviors (Krebs & Davies 1978) ; however male contest competition may also be involved (Andersson 1994). Moreover, as females are usually not synchronized in their periods of sexual activity, and only a small proportion of them will visit the male aggregation at any time, inter-male competition for mates is thus intense and mating success often varies greatly among the males on a lek (Andersson 1994). Sexual selection and dimorphism are thus expected to be stronger in lekking than in other related species (Darwin 1871).

In the case of resource defence polygyny (territoriality), male behavioral interactions readily interpreted as active defence (advertisement, threat, and attack) of the territory may be infrequent and several authors have emphasized the importance of a subjective boundary modifying behavior inside and outside the delineated area, or talked about a dominance depending on location with a reciprocity of dominance among neighboring territory holders (see Owen-Smith 1977, Geiger & Krämer 1974, Kitchen 1974). Territorial systems should thus provide the conditions in which intrasexual selection will favor the enhancement of characters needed mainly for assessing male dominance, status and fighting ability, and for successfully defending the territory without involving fights (Krebs & Davies 1978). Moreover, female choice should be mainly directed not towards the males themselves but towards the quantity or quality of the resources that the males are defending. Mating systems of this type will thus generally not lead to the evolution of male epigamic characters through intersexual selection.

Female defence polygyny (harem and roving) may arise as an extension of resource defence polygyny, male aggressive behaviors not being directed mainly to the defense of an area but of the females attracted to that area. In this case, direct male-male interactions are common and sexual selection should be primarily intrasexual, favoring the development of characters that enhance male strength and fighting ability (Krebs & Davies 1978), while female choice may not be important.

c) Potentiality for sexual selection in territorial ungulates

In territorial ungulate species, the number of resident females present in the various male territories can vary widely. Such differences in number of potential mates seems to contribute to variability of reproductive success of individual males and the number of female ranges overlapping the territory seems to limit seasonal mating success for a territorial male (e.g., in roe deer: Liberg *et al.* 1996). According to sexual selection theory, neighboring territorial males should thus attempt to enhance their access to receptive females still further by maximizing the number of female ranges overlapping their territory. This could be done in two different, but not exclusive, ways: either by enlarging their zone of dominance, or by occupying territories in areas particularly favored by females during the main breeding period (Owen-Smith 1977), since the distribution of receptive females is influenced by variation in resource distribution in mammals. This is expected in resource defence polygyny where, by definition, males defend a resource that is attractive to females. We can thus expect that male territory size and/or habitat quality in male territory might be sexual selected traits in territorial ungulates.

But as pointed out by Balmford *et al.* (1992), male quality and territory quality are often intercorrelated, and it is often not possible to disentangle them. Indeed, intrasexual competition among males is likely to produce a situation where the most competitive males occupy the largest territories or the territories preferred by females. If characters of males that allow success in intrasexual competition are those that are sought after by females, there would be no need for females to choose among males according to male phenotypic quality. Females can simply choose the best territories, and male-male competition would ensure that those territories were occupied by the best males (Apollonio *et al.* 1990). However, it is possible that females would gain by choosing males according to characteristics (structures or behavior patterns) other than those important in intrasexual competition that could be reliable indicators of male phenotypic quality. A conflict may then exist because the preferred males would not necessarily be in the preferred territories. In this case, females should also select territories partly because of the characteristics of defending males (Apollonio *et al.* 1990). When males defend mating territories, females can therefore be attracted to them by the area itself because it contains some resources (e.g., food, shelter from predators), the males, or some component of both. In conclusion, we can expect that sexual selection in territorial species may act on male individual characteristics that enhance the fighting ability/dominance ranks of males and/or their attraction for females (e.g., body size/weight/condition and weapon/ornament size).

3. SEXUALLY SELECTED TRAITS IN MALE UNGULATES

In this section, I will attempt to give a background to the main sexually selected traits that have been reported in male ungulates, focusing mainly on territorial ungulates and with special reference to Cervidae, Bovidae and Antilocapridae (see appendice 1). The main criteria for the inclusion of a study in this review was that it demonstrates a statistically significant relationship between the quantitative variation in a character and mating success. In a few cases however, despite the lack of such a demonstration, some studies, for which results strongly suggest a role of a character in male contests or female choice, have also been included.

a) Body size, body mass and body condition

Larger male than female size, typical of most birds, mammals (especially in ungulates), and some reptiles, amphibians, beetles, crustaceans, and certain other groups, has usually been explained by a size advantage in contests over females (e.g., Darwin 1871).

Studies of a wide variety of vertebrate species, in which fights are decided by contests involving pushing, have thus found that larger male size often gives an advantage in dominance contests and fights over females. However, few of them have clearly shown that dominance also leads to higher production of offspring (reviewed by Clutton-Brock 1988). For instance, Mc Elligott *et al.* (2001) have shown in fallow deer that male mating success was directly related to body size and that there is an indirect relationship between mating success and male body mass via prerut dominance rank. In Soay sheep too, body size is influential in determining access to females and should be a significant predictor of siring success, regardless of the size of their testes and horns (Preston *et al.* 2003). In bighorn sheep, Coltman *et al.* (2001) showed that mating success is positively correlated with body weight within and across years. In red deer finally, body size and body weight also affect reproductive success. Stags that were considerably lighter than their opponents usually lost contests. Though not all large stags were good fighters, individuals that were consistently successful in fights and held large numbers of hinds in several seasons were almost always of more than average size (Clutton-Brock *et al.* 1982). Evidence for a relationship between body size and reproductive success was also provided by the fact that lifetime reproductive success among stags was well correlated with mean antler weight, which is known to be related to body size and weight in red deer (e.g., Clutton-Brock *et al.* 1979).

But large size may also give an advantage in endurance rivalry, permitting a male to spend longer time especially at a breeding site and compete for females (Bartholomew 1970). In Soay sheep for instance, Preston *et al.* (2003) suggested that body condition is important in determining mating success. Indeed, before gaining access to receptive females, males spend a lot of time roving, trying to locate females, and examining ewes for signs of oestrus. This time is particularly costly in terms of energy: males are estimated to lose 30% of their body weight by the end of the rut. Thus, physical exhaustion may limit the success of males in poor condition to find receptive females. In red deer too, stags in poor condition seldom rutted successfully since they often failed to secure harems, and Clutton-Brock *et al.* (1982) suggested that body condition determines male reproductive success.

Furthermore, male body size has been reported to be related to mating success, via sequestering of females and forced copulation, or sperm competition if large size leads to higher sperm production (Wedell 1997, cited in Mc Elligott *et al.* 2001). Sperm competition has been noted for instance in Soay sheep (Preston *et al.* 2003). The authors found that larger testes are independently associated with both higher copulation rates and increased siring success.

Finally, another advantage would be female preferences for large males, for example because larger males may provide more resources than smaller males or because body size may be a honest signal of genetic quality of the male (see Andersson 1994 for review). A study of genetic variability in the major histocompatibility complex in white-tailed deer suggested thus that body size may provide an advertisement of heritable male quality (Ditchkoff *et al.* 2001) and so females may act on this cue to select mates (Ditchkoff *et al.* 2001).

b) Weapon size and asymmetry

Ungulate antlers and horns have received enormous attention since Darwin (1871) developed his theory of sexual selection, and several hypotheses have been proposed to explain their evolution (e.g., Clutton-Brock 1982, Geist 1966, Lincoln 1992 for reviews), in the framework of male competition over females.

A widespread idea is that horns and antlers in ungulates are used as weapons against rival males during the mating season (e.g., Darwin 1871, Geist 1966). Large horn and antler size (irrespective of age, body size, condition and testes size) is often associated with increased access to receptive females due to the advantage that they confer in intrasexual combat. Death and high levels of damage due to fighting have been reported several times among ungulates (e.g., in red deer: Clutton-Brock *et al.* 1979). But horns and antlers could also function defensively, acting as shield (e.g., Geist 1966, Clutton-Brock 1982). The behavioral advantage of large horns and antlers should translate into reproductive success, with larger-horned and larger-antlered males siring more offspring. Clutton-Brock (1982) demonstrated that in red deer the antler’s weight was well correlated with reproductive success. But mean antler weight is known to be related to body size and weight in red deer (Clutton-Brock *et al.* 1979). However, Kruuk *et al.* (2002) showed that antler size, which are used by males as weapons in fights over access to females, was significantly correlated with male breeding success in red deer, in a given year but also across an individual’s lifetime, and both before and after correcting for body size. Besides, experimental removal of antlers reduces reproductive success in male red deer and reindeer via a reduction of their fighting ability and dominance status (Espmark 1964, Lincoln 1972, Clutton-Brock *et al.* 1982). This indicates that antlers are important in competition among males, even if other factors such as age, body size, and condition also play a role. It has also been shown that the number of offspring sired in a given year increases with male horn size in bighorn sheep (Coltman *et al.*

2001) and in Soay sheep (Preston *et al.* 2003). In muntjac, Barrette (1977) demonstrated that antlers clearly play a role as weapons in intrasexual competition over female access. In roe deer finally, a positive correlation has been found between antler size and yearling dispersal tendency, due to male-male aggression, which is directed mainly against the most sexually mature yearlings, as antler size is also correlated with testicle size (Wahlström 1994). Subadults with well developed antlers are more frequently harassed by territorial males than subadults with poorly developed antlers, supposing that the former are a bigger threat in terms of mating competition.

While large horns and antlers are efficient weapons in fights between males, they may also be used in display for intimidating opponents (e.g., Geist 1966, Lincoln 1972), functioning as indicators of male strength and fighting ability for other males. Horn and antler size is correlated with body size and nutritional condition, and hence probably also with strength (e.g., Clutton-Brock *et al.* 1982). Males might therefore assess each other in part by the size of horns and antlers, avoiding fights with superior competitors (e.g., Geist 1966, Clutton-Brock *et al.* 1982). Geist (1966) put forward that this may be the case in bighorn sheep. In reindeer, Barrette & Vandal (1990) distinguished between fighting (which is very violent, occurs between matched males, can cause injury and death, and is quite rare) and sparing (which usually starts slowly and is gentle, the animals carefully adjusting their antlers before pushing and twisting). In sparring, the animals with the smallest antlers initiated about half of the matches, but withdrew in almost 90% of them. The authors suggested therefore that frequent sparring could be a form of tactile assessment of fighting ability, which might later permit visual assessment of other males based on their antler size. So antlers in reindeer may play a role in male assessment of competitors. In roe deer finally, Liberg *et al.* (1996) found a correlation between a measurement of dominance and mating success in roe bucks, indicating the importance of male quality; but they found no correlation between mating success and conflict frequency, i.e. bucks that were involved in many conflicts irrespective of outcome, were not better or worse than bucks that lived more peacefully. In fact, one of the most successful bucks, that had three consecutive mating seasons, with a high number of overlapping females, and high tending and copulation scores, was never seen to interact with any competitor, simply because the author never saw any other bucks in or near his territory. His territory must have been very attractive, and the only reason for the absence of intruders may be that this male was so superior in strength that no competitors bothered or dared even to approach him. The antler size could so play a major role in the dominance hierarchy between males, acting as intimidation weaponry: males with small antlers could remain subordinate to males with larger antlers during interactions.

Finally, large weaponry in ungulates may be preferred by females, as an indicator of male quality, sexual vigor or condition (e.g., Darwin 1871) and cervid females would selectively breed with large-antlered males. Choosing a male with large weapons might thus lead to immediate benefits for females, such as a reduced risk of being courted by young, inexperienced males with inept mating behavior that may harm the females (Clutton-Brock *et al.* 1982). By responding only to males who have fully developed epigamic characters and who display vigorously and persistently, females ensure that they mate with fully mature and sexually competent males. Choosing a male with large antlers that reflect good condition, a female might also make it more likely that her offspring will be of high quality, to the extent that it is heritable. But there is, however, few evidence in mammals that females choose a mate in relation to the size of his weapons (Clutton-Brock 1982). According to Clutton-Brock *et al.* (1989), females, in fallow deer, may choose mates on the base of male antler size. A study of genetic variability in the major histocompatibility complex in white-tailed deer suggests also that antler development may provide an advertisement of heritable male quality (Ditchkoff *et al.* 2001a) and so females may act on this cue to select mates. Geist (1966) also suggested that horn size in bighorn sheep serves in intersexual selection. But there is no evidence that antlers are subject of female choice in red deer (Clutton-Brock 1982).

Sexual selection is, moreover, often associated with asymmetry, with symmetric individuals enjoying improved mating success (Møller & Thornhill 1998), and this effect seems greater than that for size of the same characters (Thornhill & Møller 1998). Fluctuating asymmetry (FA) refers to small random deviations from perfect bilateral symmetry in the development of a morphological trait (such as weapons and ornaments), normally distributed around a mean of zero (Van Valen 1962). Under the hypothesis that the degree of FA in secondary sex traits reflects the ability of males to cope adequately with environmental stress or physical damage during the development of the character, FA should reflect male quality and so might be used by females in intersexual selection to select mates, or by males in intrasexual selection to infer competitor quality. If the trait development (e.g., antler size) reflects individual quality, a negative relationship is expected between this trait development and the degree of FA (Møller 1992). Several studies have thus found a negative relationship between FA and weapon size, showing thus that the degree of FA in antler or horn size can reflect individual quality, but few of them controlled for age and body mass (Kruuk *et al.* 2003). Examination of FA in moose antlers reveals that asymmetry is less and number of antler points is greater in large-antlered males, which presumably do most of the breeding (Solberg & Saether 1993, Bowyer *et al.* 2001), but there was a negative relationship between FA and the carcass mass of an individual after correcting for antler size and this relationship changed with age. In reindeer too, the degree of FA antlers is negatively related with antler size and is positively correlated with parasite burden, so antlers could be visual indicators of individual quality (Markusson & Folstad 1997). In roe deer, absolute FA significantly decreased with age. It also tended to decrease with antler size at constant carcass mass and within age classes. Antler development could therefore represent a reliable signaling of individual quality (Pélabon & Van Breukelen 1998). According to Ditchkoff *et al.* (2001b), FA of antlers of white-tailed deer follows patterns predicted for sexually selected traits, so may be reliable signals of male quality and, as such, may be important in maintaining honesty in intrasexual advertisements during breeding. Yet some studies have reached opposite conclusion, for instance in mountain goat and bighorn sheep, in which asymmetry in horn size did not reflect individual quality in males (Côté & Festa-Bianchet 2001, Fitzsimmons *et al.* 1995). Besides, almost no studies have tested for a direct association between FA in male weaponry and mating success in ungulates or have investigated whether females select mates based on FA (Kruuk *et al.* 2003). While Malyon & Healy (1994) report a negative association between measures of FA and dominance rank in eight farmed fallow deer, Pélabon & Joly (2000) found no association between levels of asymmetry and dominance rank in a sample of 45 male fallow deer in a zoo population. Miura (1984) found that the rank of sika deer males was directly related to the configuration of the antlers. In red deer, it seems on the contrary that FA in male antler size did not predict either annual or lifetime breeding success (Kruuk *et al.* 2003).

c) Territory size, location, and habitat quality

The importance of habitat quality and territory size for male reproductive success is well documented in birds (e.g., Verner & Wilson 1966, see also Anderson 1994). It has also been suggested in a few ungulates, but data on male lifetime reproductive success are lacking in most of these studies to demonstrate the relationship between territory size, location or habitat quality, and male fitness. For pronghorns, in which males defend feeding territories, Kitchen (1974) demonstrated thus a positive correlation between forage quality in a territory and the mean number of females present or male mating success. In a fallow deer lek in Italy, females appear to choose mates partly on the basis of location, and thus males should compete for ownership of territories preferred by females (Apollonio *et al.* 1990). In a population of red deer with harem mating system, male reproductive success was affected by the area where the stag rutted (Clutton-Brock *et al.* 1982). At Kilmory and Samhnan Insir, where large numbers of hinds gathered on the greens, the reproductive success and harem size of stags was higher than in the Intermediate Area or the Upper Glen, where there were fewer hinds. In a population of red deer with resource defence polygyny, Carranza (1995) fenced territories so that the territorial males had to defend a new territory at a different site. He showed that females are attracted by the area rather than by the male, and therefore the success of a territorial male largely depends on the location of his territory. In roe deer finally, the quality of the territory, but not territory size, seems to influence male mating success according to Liberg *et al.* (1996), and males with clover fields in their range had the highest success .

d) Other potential sexually selected traits

- **Chemical signals**

It has long been known that scent is used for mate attraction in insects, and for territorial marking in mammals (e.g., Gosling 1982). Many male mammals scent-mark their home range or defended territory. Territorial scent marking might play a role in attraction or physiological priming of mates, especially in some small mammals, which could play important roles in reproductive competition and sexual selection. Females might discriminate among males in relation to their odors (for example between dominant and subordinate males). Odors from adult males may also accelerate puberty in juvenile females, induce oestrus and ovulation and facilitate pregnancy in adult females, delay puberty in juvenile males, and perhaps reduce testosterone levels in other adult males (Andersson 1994). For the male, such effects on females should often increase his mating and fertilization success. Several aspects suggests that male scent marking may also be related to contest competition over mates (Andersson 1994). Males mark more than females, dominant males and territory holders mark more than others, and males often mark conspicuously during contests with others (Ralls 1971). Scent marks may thus function in competitor assessment (e.g., Gosling 1982). In moose, males dig rutting pits where they deposit odorous urine and females are strongly attracted to and often wallow in those pits. Moreover, mating and parturition are highly synchronized in this species. Whittle et al. (2000) suggested that male urine may play an important role in the mating system and in synchronizing reproduction in moose. The authors analyzed male urine, and found potential pheromones. They suggested that these compounds are related to hypophagia and catabolism of body reserves by rutting males, and thereby provide an honest advertisement of body condition by male moose during the mating season. In white-tailed deer, Miller et al. (1998) found some differences in compound presence and concentration of volatiles in urine between dominant and subordinate males and suggested that these differences may produce a rank-specific odor and may serve in the identification of social status in this species.

- **Acoustic signals**

Song and other acoustic signals are the traits most often shown to be sexually selected, especially in insects, frogs, and birds (see review in Andersson 1994), but also in some mammals. Acoustic signals may be used in contests between males but also for attracting females (Darwin 1871), as the territory is important for mating success. In wild red deer, male roaring rates reflects male condition and is positively correlated with fighting ability and reproductive success through contest competition (Clutton-Brock & Albon 1979, Clutton-Brock *et al.* 1979) and also with female choice. In two-choice loudspeaker tests with farmed red deer, females were attracted to high roaring rates and to leading bouts of roars (Mc Comb 1991). In another experiment, females exposed to playback of roaring ovulated earlier than control females (Mc Comb 1987). This suggests that roaring may enhance male success both by attracting hinds and by making them more likely to ovulate and mate before being taken over by another stag. Reby *et al.* (2001) have also shown, by conducting playback experiments, that hinds are able to discriminate between roars of their current harem-holder stag and those of other neighboring stags and suggested that this ability may be important in female mate choice in red deer. In roe deer finally, Reby *et al.* (1999) suggested that barking is linked in part to the expression of territoriality among bucks, and may enable them to identify and locate each other, and perhaps to assess dominance status, particularly during barking / counterbarking sessions involving several animals. It seems indeed that individual differences in propensity to bark are related to dominance.

Discussion / Conclusion

I have identified several traits that may be subject to sexual selection in ungulates (see section 3). A difficulty in such an exercise is to isolate indirectly selected traits from directly selected traits: a trait correlated with mating success may indeed be indirectly selected through correlation with some other, directly selected trait (Andersson 1994). It is also often difficult to separate the roles of mate choice and contests over mates in sexual selection of a trait (Andersson 1994). For example, antlers and horns in ungulates can be used both as weapons and/or as ornaments, and both roles can lead to the selection of their size and symmetry. It seems however that some traits are favored mainly by one of the two mechanisms of competition over mates (see appendice 1). In ungulates, large body size in males seems thus to be usually selected by male contests (e.g., in red deer, fallow deer, Soay sheep and bighorn sheep), and seldom by female choice (e.g., in white-tailed deer). Acoustic and chemical signals are often selected by female choice, sometimes by both female choice and male contests, but seldom just by male contests (e.g., barking in roe deer). Finally, male territory size, location and quality are selected by only female choice.

Is it at this stage of the essay, possible to distinguish a pattern in the favored sexually selected traits and the mechanisms acting behind, according to mating tactics in ungulates? If so, do the found pattern fit to the predictions based on sexual selection theories (see section 2)? To answer to these questions, I will compare the results of three cervid species with contrasting mating tactics: red deer (female defence polygyny), fallow deer (lek) and roe deer (resource defence polygyny).

In the harem defence red deer, male contests seem to be the main mechanism of sexual selection, whereas in the lekking fallow deer and the territorial roe deer, both mechanisms of competition over mate (intra and intersexual selection) seem to coexist. These results therefore fit well with the predictions.

Moreover, in the harem species (i.e., red deer), the traits that are reported to be selected by intrasexual selection are body size/weight/condition and antler size, which may enhance male strength and fighting ability. This is actually expected for female defence polygyny species. However, female choice may also play a role in competition over mates, via roaring rate and rut location. In the territorial species (i.e., roe deer), antler size/symmetry and barking seem to be selected and are favored by male contests. These traits are known to be important in the defence of the territory by allowing the assessment of male dominance, status or fighting ability by other males without direct interactions. Besides, territory quality in roe deer is selected by female choice, whereas male traits (e.g., body size) seem not to be subject to intersexual selection. This is also expected in resource defence polygyny species. Finally, for the lekking species (i.e., fallow deer), male ornament development seems to be selected by intersexual selection, but intrasexual selection may also play a role in this development. Besides, male contest competition over mates may also be involved in the selection of body size, while male position on the lek could play a role in male attractiveness, with a preference for central males as noted in many lekking species (see Andersson 1994 for a review).

The results in these three contrasting species seem therefore to fit on the whole with theoretical predictions. But more empirical data are required in order to generalize to the whole ungulate taxa. Further, we need more studies on a whole variety of potentially selected traits, in different species within a range of mating tactics to better understand the influence of sexual selection on male mating systems in mammals in general and in ungulates more specifically.

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Appendice 1. Sexually selected traits reported in ungulate species mentioned in this essay.

Species		**Mating system**	**Trait selected**	**Selective mechanism**	**Reference**
Red deer	*Cervus elaphus*	Harem	Body size/weight	Male contests	Clutton-Brock *et al.* 1982
			Body condition	Endurance rivalry	Clutton-Brock *et al.* 1982
			Roaring (rate)	Female choice/Male contests	Clutton-Brock *et al.* 1979, Clutton-Brock & Albon 1979, Mc Comb 1987, 1991, Reby *et al.* 2001
			Antler size/weight	Male contests	Clutton-Brock 1982, Kruuk *et al.* 2002
			Rut location	Female choice	Clutton-Brock *et al.* 1982, Carranza 1995
		Territoriality	Territory location	Female choice	Carranza 1995
Fallow deer	*Dama dama*	Lek	Body size/weight	Male contests	Mc Elligott *et al.* 2001
			Antler size/weight	Female choice	Clutton-Brock *et al.* 1989
			Antler symmetry?	Male contests	Malyon & Healy 1994
			Position on lek	Female choice	Apollonio *et al.* 1990
Roe deer	*Capreolus capreolus*	Territoriality	Antler size/weight	Male contests	Wahlström 1994, Liberg *et al.* 1996
			Antler symmetry	Female choice/Male contests	Pélabon & Van Breukelen 1998
			Barking	Male contests	Reby *et al.* 1999
			Territory quality	Female choice	Liberg *et al.* 1996
White-tailed deer	*Odocoileus virginianus*	Roaming	Antler size/weight	Female choice	Ditchkoff *et al.* 2001a
			Antler symmetry	Female choice/Male contests	Ditchkoff *et al.* 2001b
			Urine pheromones	Female choice/Male contests ?	Miller *et al.* 1998
			Body size/weight	Female choice	Ditchkoff *et al.* 2001
Moose	*Alces alces*	Roaming	Antler symmetry?	Female choice	Solberg & Saether 1993, Bowyer *et al.* 2001
			Urine pheromones	Female choice	Whittle *et al.* 2000
Reindeer	*Rangifer tarandus*	Harem	Antler size/weight	Male contests	Epsmark 1964, Barrette & Vandal 1990
			Antler symmetry	Female choice/Male contests	Markusson & Folstad 1997
Sika deer	*Cervus nippon*	Territoriality	Antler symmetry	Male contests	Miura 1984
Reeves's Muntjac	*Muntiacus reevesis*	Territoriality	Antler size/weight	Male contests	Barrette 1977
Soay sheep	*Ovis aries*	Roaming	Body size/weight	Male contests	Preston *et al.* 2003
			Body condition	Endurance rivalry	Preston *et al.* 2003
			Horn size	Male contests	Preston *et al.* 2003
Bighorn sheep	*Ovis canadensis*	Roaming	Body size/weight	Male contests	Coltman *et al.* 2001
			Horn size/weight	Female choice/Male contests	Coltman *et al.* 2001, Geist 1966
American pronghorn	*Antilocarpa americana*	Territoriality	Territory quality	Female choice	Kitchen 1974

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