Sexual selection and social rank in bighorn rams

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For many ungulates, male reproductive success increases with social rank. Because rank is established through contests, it should be correlated with individual mass and select for high sexual dimorphism in body mass. It is difficult to weigh free-ranging ungulates, however, so empirical data on the relation between mass and social rank are scarce. We monitored individual mass and social rank of marked bighorn rams, *Ovis canadensis*, at Sheep River, Alberta, Canada over 5 years. Each year, rams were organized in a linear hierarchy. Social rank increased with age, and rank in one year was a good predictor of rank in the next year. The stability of dyadic relationships increased with the difference in age of individuals in the dyad but decreased as rams aged. Until about 6 years of age, the positive effects of age and individual mass on social rank were indistinguishable, because rams gained mass each year. The relation between body mass and social rank strengthened with age, probably because, after the heavier rams attain their lifetime asymptotic weight, they can challenge older conspecifics. In mature bighorn rams, social rank is a major determinant of reproductive success. By providing evidence that mass is an important determinant of rank, our study supports the contention that sexual selection leads to high sexual dimorphism in this species.

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Sexual selection requires a correlation between fitness and the expression of a phenotypic trait associated with mate acquisition (Andersson 1994). In polygynous species, yearly reproductive success of males is often skewed, because a few males mate with many females and several males do not mate at all (Hogg & Forbes 1997; McElligott et al. 2001; Coltman et al. 2002; Preston et al. 2003). In these species, male reproduction is largely determined by intrasexual competition for mates (Andersson 1994). Sexual selection should therefore affect traits linked to success in male–male contests, including body size and weapons such as antlers, horns and spurs (Andersson 1994; Coltman et al. 2002; Preston et al. 2003). Escalated fights are costly in terms of physical injuries or in time and energy expenditure (Maynard Smith 1974; Clutton-Brock et al. 1979), so reliable noncontact assessment of relative fighting ability would benefit both contestants (Côté 2000). The establishment of dominance relationships may limit the frequency of fights and associated injuries (Rowell 1974). Here we used the definition of dominance proposed by Drews (1993): an attribute of the pattern of repeated aggressive interactions between two individuals (a dyad), characterized by an outcome in favour of one individual. Social rank refers to the relative position of an individual in the dominance hierarchy that may develop within a group.

The reproductive success of males of several ungulate species increases with social rank (Clutton-Brock et al. 1979; Lott 1979; Clutton-Brock et al. 1982; Hogg & Forbes 1997; Wolff 1998; McElligott et al. 2001). Rank is a strong correlate of male fitness, so it is important to investigate which individual characteristics affect social rank and to determine how dominance relationships vary over the lifetime of individuals. High social rank is achieved by challenging other individuals in dominance fights (Barrette & Vandal 1986; Drews 1993). Consequently, individual characteristics likely to give a competitive advantage during contests should increase a male's rank. The size of weapons such as antlers and horns should be important during contests (Coltman et al. 2002; Preston et al. 2003). Age is often correlated with social rank for both male (Hass & Jenni 1991; Wolff 1998; Pelletier et al. 2003) and female ungulates (Rutberg & Greenberg 1990; Festa-Bianchet 1991; Côté 2000). Older individuals are typically larger and have larger weapons, but they could also be more experienced than younger ones, and experience could confer a competitive advantage during contests. For females, age has an overwhelming role in determining dominance, possibly because dyadic relationships established early in

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life (when there are large age-related differences in size) are maintained in later years, even though the difference in size between members of a dyad may disappear or even be reversed (Thouless & Guinness 1986; Côté 2000). The ontogeny of dyadic relationships as individuals age has not been investigated in males, but the fitness benefits of dominance are probably much higher for males than for females after body growth is completed, so age should be much less influential in determining dominance in males than in females.

Although body mass is generally considered to be the main determinant of social rank in male ungulates (Andersson 1994; McElligott et al. 2001), few studies have measured the yearly body mass of marked individuals of known age while monitoring their social behaviour. In addition, little is known about the determinants of individual rank of males in any ungulate (McElligott et al. 2001), in particular about how and why rank may change from year to year for the same individual.

We first examined the development and structure of social hierarchies in bighorn rams, *Ovis canadensis*, over a 5-year period. We tested whether yearly dominance matrices were linear and examined the between-year stability of social rank within and between cohorts. We also investigated how a ram's rank changed over its lifetime. We then investigated what individual characteristics affected the social rank of rams 2 years and older, focusing on body mass and age.

Bighorn sheep are polygynous and sexually dimorphic; in our study area in autumn, mature rams weigh about 75% more than adult ewes. The yearly reproductive success of males is highly skewed, with 10–15% of rams obtaining up to 50–60% of paternities assigned within a year (Hogg & Forbes 1997; Coltman et al. 2002). The top-ranking ram among those courting an oestrous ewe will guard ('tend') that ewe against all other rams. Tending is the most successful mating tactic in this species (Hogg 1984, 1987). An alternative tactic, 'coursing', is used by surbordinate rams (Hogg 1984) who attempt to separate the tending pair by physically attacking the tending ram. After separating an oestrous ewe from the tending ram, coursing rams will chase her and attempt to copulate before the tending ram can regain control (Hogg 1984). Coltman et al. (2002) found that in the Ram Mountain population, mass and horn size of males were correlated with yearly reproductive success, but they had no data on the social rank of rams. In our study population, a male's social rank was a good predictor of yearly reproductive success (Hogg & Forbes 1997; Hogg 2000). We previously reported that social rank was related to testosterone levels but that relation disappeared when age was accounted for (Pelletier et al. 2003). Hass & Jenni (1991) suggested that male bighorn rams form a linear hierarchy where social rank increases with age.

METHODS

Study area and Population

We studied bighorn sheep in the Sheep River Provincial Park, Alberta, Canada (50°40′N, 114°35′W, elevation 1450–1700 m). Since 1981, sheep have been captured at 4–6 months of age and marked with plastic eartags. Consequently, their exact age is known and more than 95% of resident sheep are individually recognizable (Festa-Bianchet 1986a; Hogg & Forbes 1997). The rut is in late November and early December. In October and early November, rams form a pre-rut congregation, often with all males present in the park together in a single group (Festa-Bianchet 1986b; Pelletier & Festa-Bianchet 2004). During the pre-rut, rams interact frequently and establish social status which, for mature rams, is the main determinant of access to oestrous ewes during the rut (Hogg 1984, 1987). From 2000 to 2004, during the pre-rut, the park was searched on foot and groups of rams were observed from at least 75 m with Bushnell spotting scopes (15–45×) or Leica binoculars (10×). All rams were either marked (yearly range 81–94%) or known individually through horn shape and size. Interactions were collected ad libitum or during continuous activity budget observation periods lasting 6–10 h (Pelletier & Festa-Bianchet 2004).

Social Rank

Six types of social interactions were recorded: front kick, horn rubbing, mount, frontal clash, butt and noncontact displacements (Geist 1971; Hogg 1987; Hass & Jenni 1991; Pelletier et al. 2004). When an encounter between two individuals included repetition of the same behaviour (e.g. repeated frontal clashes), we recorded only one interaction every 15 min. Only rams 2 years and older seen interacting with at least five other rams were included in the yearly matrix. We included data on yearlings when examining the relationship between age and mass, but we excluded them from other analyses because yearlings spend most of their time in female nursery groups, occasionally interacting with 2-year-olds (Ruckstuhl & Festa-Bianchet 2001) but rarely interacting with older rams.

Body Mass

Beginning in 2001, we lured rams onto a platform scale baited with salt (Bassano et al. 2003) to weigh them during October and early November. Repeated weighing of the same individuals suggested that mass was stable during that time (Pelletier & Festa-Bianchet 2004) and consequently we did not adjust body mass according to measurement date. For rams weighed more than once in the same year, we used the average mass. We obtained 67 yearly weights over 4 years ($N = 30$ rams).

Statistical Analyses

As suggested by de Vries (1998), we ordered individuals in yearly dyadic interaction matrices and calculated the linearity of yearly hierarchies using the linearity index h' (de Vries 1995), which is based on the Landau index (Landau 1951) and varies between 0 and 1, where 1 is perfectly linear. A randomization procedure (10 000 randomizations) suggested that the h' index was significantly linear in all 5 years (Table 1). Because the assumption of linearity was

Table 1. Descriptive statistics of dominance matrices of bighorn sheep rams 2 years and older, from 2000 to 2004, Sheep River Provincial Park, Alberta, Canada

Year	Number of males	Interactions observed	% of dyads observed	h'*	P†	DC‡
2000	21	261	49.0	0.33	0.003	0.94
2001	23	737	67.6	0.48	<0.001	0.93
2002	27	741	60.4	0.42	<0.001	0.96
2003	23	652	71.1	0.57	<0.001	0.95
2004	25	464	60.7	0.37	<0.001	0.94

*Linearity index (see text for details).
†P value associated with the linearity test using h' index, based on 10 000 randomizations.
‡Directional consistency index in encounter outcome (see text for details).

met, we then ranked individuals using a two-step procedure, which minimized first the number and then the strength of inconsistencies (de Vries 1995, 1998; Côté 2000). The directional consistency (DC) index was also calculated to estimate the predictability in the outcome of encounters within each dyad. The DC index ranges from 0 to 1 (0: the outcome of interactions within a dyad is unpredictable based on earlier encounters; 1: complete directionality in encounter outcome; van Hooff & Wensing 1987). The DC is calculated across all dyads as the total number of times that an encounter ended with the most prevalent outcome within each dyad, minus the number of times its outcome was the opposite, divided by the total number of encounters for all individuals. All procedures were implemented in Matman 1.0 for windows (Noldus Information Technology 1998). The number of rams in yearly matrices ranged from 21 in 2000 to 27 in 2002 (Table 1); therefore, we transformed social rank as suggested by Côté (2000), using the algorithm $1 - (\text{rank}/Nx)$, where Nx is the number of rams in the year x.

We used Pearson correlations to assess stability in social rank between years. Our data contain repeated observations of the same individual over time; therefore, to investigate the relation between rank, age and body mass, we used linear mixed models including ram identity as a random term (Pinheiro & Bates 2000) thereby controlling for pseudoreplication. The individual effect was tested by comparing the log likelihood of models with and without the random term (Steele & Hogg 2003). Identity was always significant and therefore was included in all analyses. Error terms of all models presented a normal distribution and homogeneous variance.

RESULTS

Mechanics of Social Rank

Most of the 2855 agonistic encounters observed between rams involved dominance reinforcement ('front kick' accounted for 37% of interactions) and submissive behaviour (rubbing of a subordinate's preorbital gland on the horn or face of a dominant ram, 46% of interactions).

Males also used frontal clash (2% of cases), butting (5%), homosexual mount (4%) and noncontact displacement from a foraging or a bedding site (6%). Escalation of contest was rare: only eight dominance fights involving repeated frontal clashes were observed during 5 years (>600 h of observations each year). Bighorn rams formed a linear hierarchy, and in all years, the outcome of encounters within a dyad was highly consistent; the range of the directional consistency index was 0.93–0.96 (Table 1). For rams 2 years and older, rank in one year was a strong predictor of rank in the following year: correlations between rank in consecutive years ranged from 0.93 to 0.97 and were all highly significant ($P < 0.001$, $N = 12–20$).

To assess stability in social rank between individuals, we examined long-term changes in dyadic relationships for individuals observed interacting during 2–5 consecutive years. For 150 dyads within the same cohort, the winner remained the same in 76% of cases ($N = 114$); in 24% of dyads ($N = 36$), the formerly dominant ram became subordinate at some point during its lifetime. The lifetime stability of dyadic relationships increased with the difference in age between members of the dyad. For rams whose age differed by 1 year, dyads maintained the same winner in 90% of cases ($N = 167$). The proportion of dyads that maintained the same relationship over the lifetime increased to over 99% ($N = 130$) when the difference in age was 2 years, and to 100% ($N = 121$ dyads) when it was 3 or more years.

To examine how rank may change within a dyad according to both the age difference and the absolute age of the two rams involved, we examined the age-specific probability of rank switch within dyads with up to 3 years difference in age (Fig. 1). Rams in the same cohort were more likely to switch in rank between years than were rams from different cohorts. Rams 1 year apart were more likely to switch rank as they aged (Fig. 1). For dyads with 1 year difference in age, 14 of 16 dominance reversals observed involved a formerly subordinate younger ram that became dominant.
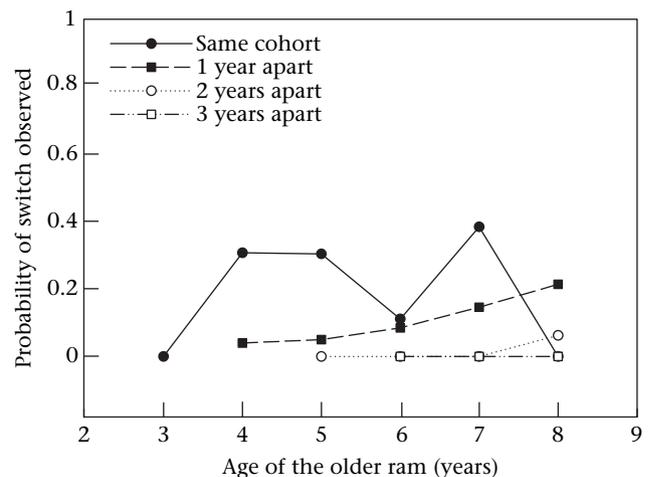

Figure 1. Probability of dominance reversal over consecutive years for dyads of bighorn rams aged 2 years and older according to the absolute difference in age between the members of the dyad.

Determinants of Social Rank

Most rams appeared to reach an asymptotic autumn mass of 135–140 kg at about 6 years of age, but some reached this mass when as young as 4 years (Fig. 2). Both mass and age were highly correlated with social rank, although the shapes of these relations were inverse (Figs 3a, b). Mass, age and rank were all highly correlated (Figs 2, 3), so we could not examine them together in a multiple regression without multicollinearity problems (Glantz & Slinker 1990). Males first use tending as a mating tactic at about 6 years of age, and for tending rams, social rank is a strong determinant of mating success (Hogg & Forbes 1997). Therefore, we analysed the effects of age and mass on rank according to male age. We compared the correlations between rank and age and rank and mass for rams aged 2–5 years, when mass was highly correlated with age ($F_{1,28} = 740.55$, $r^2 = 88.9$, $P < 0.001$), and for rams aged 6 years and older, for which mass was independent of age ($F_{1,11} = 0.777$, $r^2 = 0.07$, $P = 0.4$). For rams aged 2–5 years, mass explained 68% of variance in rank ($F_{1,19} = 82.41$, $P < 0.001$) and age explained 77% ($F_{1,19} = 152.51$, $P < 0.001$). For males 6 years and older, we used a linear model instead of the linear mixed model because we had a small sample size ($N = 13$) and only two individuals with repeated measurements. Mass explained 37% of the variance in rank ($F_{1,11} = 6.360$, $P = 0.028$), but age was not significant and explained only 12% ($F_{1,11} = 1.542$, $P = 0.24$). Although rank generally increased with age, beginning at age 5 years, a few rams dropped in rank as they aged (Fig. 4).

DISCUSSION

As reported by Hass & Jenni (1991), bighorn rams form a linear hierarchy and social rank is strongly associated with age. The positive effect of body mass on social rank seemed to increase after males reached their asymptotic
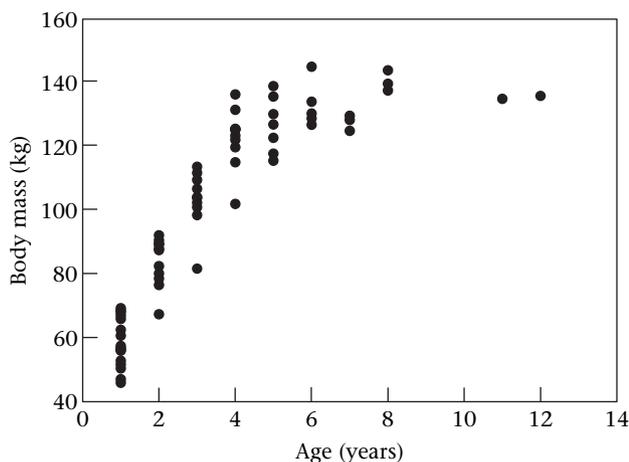

Figure 2. The relationship between body mass (kg) in early autumn and age for bighorn rams 1 year and older at Sheep River. A linear mixed model explained 91% of the variance (age: $F_{1,32} = 1206.26$, $N = 67$ observations from 33 individuals, $P < 0.001$; age^2: $F_{1,32} = 278.50$, $P < 0.001$).
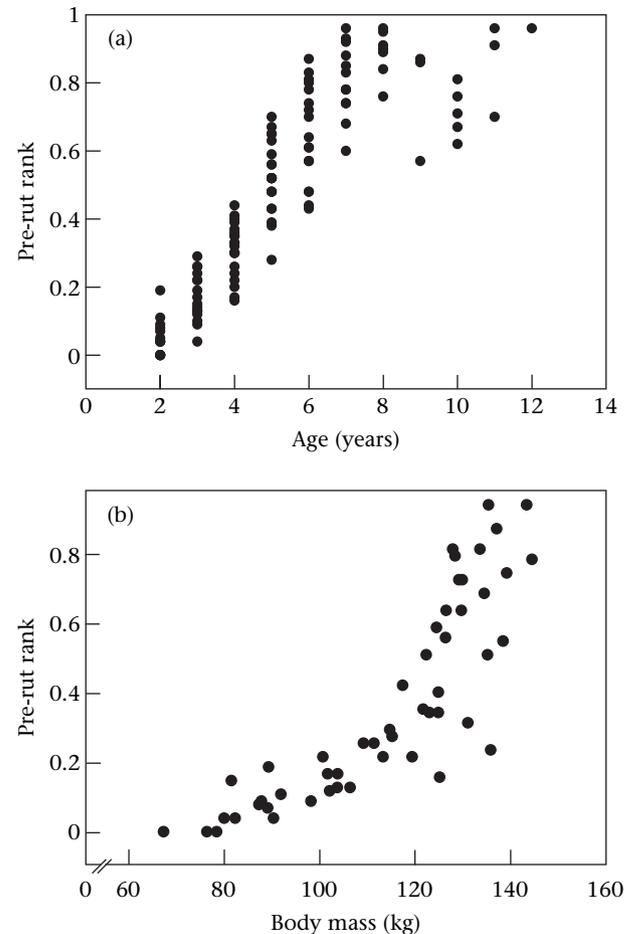

Figure 3. (a) Relationship between age and social rank for bighorn rams aged 2 years and older. A linear mixed model explained 86% of the variance (age: $F_{1,64} = 558.54$, $N = 119$ observations from 53 individuals, $P < 0.001$; age^2: $F_{1,64} = 61.02$, $P < 0.001$). (b) Relation between body mass in early autumn and social rank for bighorn rams aged 2 years and older. A linear mixed model explained 73% of variance (mass: $F_{1,23} = 118.61$, $N = 51$ observations from 26 individuals, $P < 0.001$; mass^2: $F_{1,23} = 7.85$, $P = 0.01$).
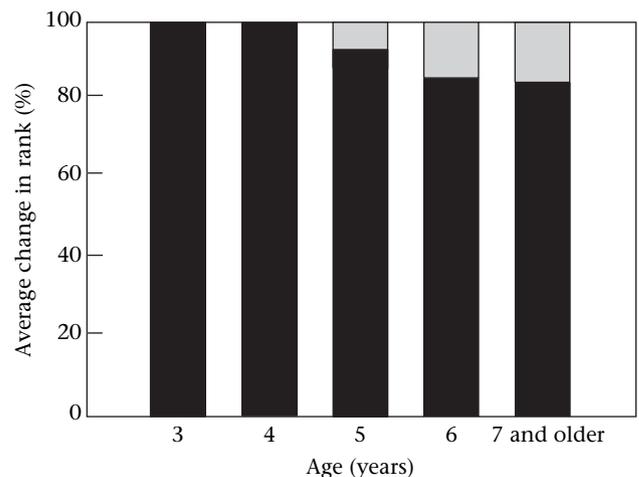

Figure 4. Individual change in social rank from the previous year for bighorn rams 2 years of age and older. ■: percentage increase; □: percentage decrease.

mass, usually between 5 and 7 years of age. By then, body mass was mostly independent of age, and individual differences in rank were determined mostly by body mass. That is because after about 6 years of age, some rams could successfully challenge older (but lighter) conspecifics, as revealed by rank reversals at the dyad level. Body mass therefore became an increasingly important determinant of social rank as rams aged, as reflected by the abrupt change in slope of the relation between mass and rank. Although age was weakly correlated with rank for males 6 years and older, age difference probably remained important throughout adulthood because experience and the outcome of previous interactions may affect social rank. Until about 5 years of age, the strong correlation between body mass and age (Fig. 2) meant that their respective effects on social rank were almost indistinguishable. Determining the exact age threshold at which the importance of mass increased is problematic because of the high variability in body mass within age groups (the heaviest 4-year-old male was 35 kg, or 34% heavier than the lightest).

The age at which rams reached their asymptotic weight coincides with the age at which some rams start to use tending of oestrous ewes as a mating tactic and therefore enjoy high reproductive success (Hogg & Forbes 1997). Our results support the suggestion that the short-term benefit of high rank is therefore limited to older rams (Hogg & Forbes 1997; Coltman et al. 2002). A small difference in mass (and therefore in social rank) for rams aged 6 or more years can lead to a very important difference in mating success, because this mass difference may determine which ram will tend an oestrous ewe and which will have to resort to coursing, a mating tactic that is much less successful than tending (Hogg 1984; Hogg & Forbes 1997) and whose success appears to be independent of rank (Hogg & Forbes 1997). The difference in fitness payoff for a given absolute difference in rank is therefore likely to be more important for rams near the top of the hierarchy (e.g. ranks 1 and 2) than for lower-ranking rams (e.g. ranks 10 and 11; Hogg & Forbes 1997). Similarly, Coltman et al. (2002) suggested that, in the Ram Mountain population, horn length had little or no influence on the mating success of rams younger than 6 years, but became an increasingly important determinant of mating success for older rams. We had few data on horn length, but it is likely that both horn and body size are important determinants of social rank. Although the short-term benefits of rank are mostly restricted to adult rams, younger rams challenge each other and establish a linear dominance hierarchy, probably to gain experience. Moreover, within a cohort, small individuals are likely to remain small as they age, because bighorn rams do not appear to be able to compensate for slow early growth (LeBlanc et al. 2001). Therefore, rank within a cohort is likely to be maintained during adulthood.

Social rank is a strong predictor of yearly reproductive success in bighorn sheep. At Sheep River, there are typically 20–35 males 2 years and older competing for access to 40–60 oestrous ewes, yet the three top-ranking males can father 50–60% of lambs in a cohort (Hogg & Forbes 1997). Coltman et al. (2002) found that the reproductive success of mature males in the Ram Mountain population was correlated with both body mass and horn length. Hogg & Forbes (1997) showed that rank was associated with mating success. These earlier studies implied that there should be a strong relation between mass and social rank, which is confirmed by our results. The fitness benefits of achieving a high rank are gained mostly after rams attain a large body mass, so bighorn rams should be selected for rapid growth early in life to reach asymptotic mass as soon as possible. That conclusion has important implications for the conservation of ungulates subject to sport hunting. In hunted populations of ungulates, the larger and older males are typically harvested by hunters, giving an artificial reproductive advantage to slow-growing males (Coltman et al. 2003; Festa-Bianchet et al. 2004) and leading to a truncated male age structure, which may affect the social structure of the population. Therefore, trophy hunting has the potential to counter sexual selection if sexually selected traits are also selected by hunters.

Although it is widely expected that there should be a direct relation between social rank and body mass in male ungulates, our study is one of the few reporting empirical data to test this relation. Clutton-Brock et al. (1979) found that red deer stags, *Cervus elaphus*, over 6 years frequently interacted with opponents that were several years older, but that stags aged 5 years and younger were more likely to interact with individuals of their own age. Clutton-Brock et al. suggested that, for males older than about 6 years, age was no longer related to body size or fighting ability, but this idea had no empirical support. Our results on the relation between rank and body mass for bighorn rams support their suggestion. McElligott et al. (2001) also found an association between rank and mass before the rut for fallow deer, *Dama dama*. They did not find an effect of age, but they restricted their analysis to males between 5 and 8 years of age, where, according to our results, one should not expect a strong age effect.

Although the probability of losing rank increased as rams in our study aged, most rams (about 90%) continued to increase in social rank until death. The oldest marked rams observed at Sheep River was 13 years old, but few males survive to 10 years, because survival rate declines after about 7 years of age (Loison et al. 1999). The decrease in rank starting at age 5 is unlikely to result from early senescence. Instead, decrease in rank is probably explained by both the weak correlation between mass and age for older males and the strong effect of mass on social rank. Once males reach about 6 years of age, they face an increasing probability that some of their younger competitors may be heavier and thus may successfully challenge them for social rank (Fig. 1).

The fitness consequences of rank for male and female ungulates differ substantially. In females, high social rank is usually associated with better access to forage (Barrette & Vandal 1986; Rutberg & Greenberg 1990; Thouless 1990; Kojola 1997), but in males it is associated mainly with mating opportunities (Clutton-Brock et al. 1979; Hogg & Forbes 1997; McElligott et al. 2001; Preston et al. 2003). Social rank is more directly related to fitness in males than in females, so one should expect stronger intrasexual competition and more frequent reversals of dyadic relationships over a male's lifetime than a female's.

Social rank in females appears to be stable over time (Côté 2000), and dyadic relationships are possibly established early in life (Thouless & Guinness 1986; Byers 1997; Guilhem et al. 2002) and then are maintained despite changes in individual characteristics such as mass (Thouless & Guinness 1986; Côté 2000). For bighorn sheep ewes, Eccles & Shackleton (1986) found no linear hierarchy, and rank was not associated with individual body mass. Festa-Bianchet (1991) found that the outcome of aggressive interactions was strongly age related, with the older ewe within a dyad winning in 92% of the cases. Interactions between ewes are rare (Eccles & Shackleton 1986; Festa-Bianchet 1991), suggesting that ewe social rank has limited fitness consequences. This idea contrasts with what we found in the same species for males, where mass seems a better predictor of rank than age for mature individuals, and rams actively and frequently interacted during the pre-rut. Therefore, we conclude that the sexual difference in the benefit associated with high social rank leads to different life-history strategies. High social rank in females gives indirect fitness payoffs, but in males social rank is an important determinant of fitness.

In conclusion, social rank in bighorn sheep is a complex trait determined by both age and mass, whose respective influences change over a ram's lifetime. Age is the principal determinant of rank for young rams, for which the short-term benefit of social rank is low. When rams reach their asymptotic weight, mass becomes the main factor affecting social rank. Rank is a strong determinant of reproductive success for mature males, so sexual selection should favour rapid growth in male body size, shortening the number of years before a ram can compete for very high social rank and therefore the opportunity to adopt the highly successful mating tactic of tending oestrous ewes. Our results support the hypothesis that sexual selection favours a high degree of sexual dimorphism in polygynous ungulates.

Acknowledgments

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