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MATING TACTICS AND MATE CHOICE IN RELATION TO AGE AND SOCIAL RANK IN MALE MOUNTAIN GOATS

JULIEN MAINGUY,* STEEVE D. CÔTÉ, ETIENNE CARDINAL, AND MÉLINA HOULE

Département de Biologie and Centre d'Études Nordiques, Université Laval, Québec, Québec G1K 7P4, Canada

In polygynous mammals, mating success of males often depends on intense male–male competition and the use of alternative mating tactics. Because reproduction incurs substantial energetic costs and risks of fight injuries, mate selection by males should be expected, particularly when females vary in their ability to produce offspring but can only be defended 1 at a time. Here, we investigated during 3 ruts how age and social rank of male mountain goats (*Oreamnos americanus*) affected the formation of consort pairs with females (''tending'' tactic) in a marked population at Caw Ridge, Alberta, Canada. Among consort pairs, we quantified the behaviors of males and females, and the use of an alternative mating tactic by competing males, ''coursing,'' which consists of disrupting the pair to gain temporarily access to the female, often by pursuing her. Mate choice was assessed by testing if old and dominant males observed in consort pairs tended experienced females more often than younger females, because reproductive success of females increases with age. Males in consort pairs were $\geq$4 years old and most (86%, $n = 59$) were in the top one-half of the dominance hierarchy. Age and social rank of males were positively related to age of females and the total number of young produced by the tended female. All observed matings ($n = 32$) occurred between 14 November and 2 December and 91% were between males and females in consort pairs. Subordinate males gained mating access to females through coursing, but this tactic was rare. Our study provides evidences of mate choice by males for experienced females in an ungulate and the 1st quantitative information on the rut of mountain goats.

Key words: alternative mating tactics, dominance, mate choice, mountain goat, *Oreamnos americanus*

In polygynous and sexually dimorphic mammals, competition is often intense among males to gain access to estrous females during the breeding season (Le Boeuf 1974; Peek et al. 1986). Male–male competition and courtship behaviors may require a large proportion of a male's energy reserves (Deutsch et al. 1990; Forsyth et al. 2005), leading to substantial reproductive costs. In addition to fat stores that can be used for reproduction (McElligott et al. 2003), the ability of males to compete for access to females is also partly determined by secondary sexual characteristics such as weapons (e.g., horns, antlers, or canine teeth) and body size (Andersson 1994), which both increase with age (Coltman et al. 2002; Preston et al. 2003). As a consequence, only a few prime-aged males reach high dominance status and secure most of the matings, especially in mammals with strong sexual dimorphism such as pinnipeds (Fabiani et al. 2004; Haley et al. 1994) and ungulates (Hirotani 1994; Wolff 1998). Thus, social rank and age, which are often positively related (McElligott et al. 1998; Pelletier and Festa-Bianchet 2006), are generally regarded as 2 major determinants of mating success for males in polygynous species of mammals.

Subordinate males may use alternative mating tactics (Gross 1996; Lidgard et al. 2005) if they cannot mate using the conventional tactic, such as defending a female against other males (i.e., mate guarding). In polygynous ungulates, the use of alternative mating tactics appears to be widespread (Coltman et al. 1999; Forsyth et al. 2005; Saunders et al. 2005). In bighorn sheep (*Ovis canadensis*), for example, males can use up to 3 different mating tactics according to their age and social rank (Hogg 1984). The most successful tactic is called tending (Hogg and Forbes 1997), and it involves the defense of a single estrous female by the most dominant male among those present (Hogg 1984). The 2 other alternative tactics are generally used by subordinate males (Hogg 1984): coursing consists of challenging or bypassing the tending male to gain temporary copulatory access to the females, often by pursuing them, and blocking, which is less common (Pelletier 2005), occurs when a male attempts to sequester estrous females from dominant males. Because social rank is strongly related to age and body mass in male bighorn sheep (Pelletier and Festa-Bianchet 2006), subordinate males are typically younger (2–5 years) than dominant males and are thus constrained to use

* *Correspondent: julien.mainguy.1@ulaval.ca*

suboptimal tactics. Although tending males gain higher mating success than coursing males, about 44–50% of the offspring can be sired by coursing males (Coltman et al. 2002; Hogg and Forbes 1997). The use of alternative mating tactics by young subordinate individuals also is known to account for a significant part of the offspring sired each year in other ungulates (e.g., Coltman et al. 1999; Saunders et al. 2005).

Because reproductive effort in male ungulates leads to substantial energetic costs (Bobek et al. 1990; Forsyth et al. 2005; Mysterud et al. 2005) and serious risks of fight injuries (Hogg and Forbes 1997; McElligott et al. 1998; Saunders et al. 2005), mate choice by males may occur to increase reproductive success. Although mate choice is generally regarded as female choice of traits in males (Andersson and Simmons 2006), it is known to occur in both sexes (Andersson 1994). For instance, males able to achieve high social rank could attempt to mate with females of high reproductive value when the opportunity arises, especially in species that can only defend a single female at a time. For example, mate choice by males has been recently reported in many species of primates (Deschner et al. 2004; Parga 2006; Setchell and Wickings 2006). Hence, male primates of high rank that concentrated their mating effort on females that were more likely to produce offspring had higher reproductive success than lower-ranking males that were unable to monopolize these females (Alberts et al. 2006). However, mate choice by males has been less studied in ungulates, except recently in Soay sheep (*Ovis aries*—Preston et al. 2005) and in bison (*Bison bison*), although with mixed results (Berger 1989; Wolff 1998).

The mountain goat (*Oreamnos americanus*) is a sexually dimorphic and polygynous alpine ungulate whose mating system appears similar to that of bighorn sheep and many other polygynous ungulates in terms of mating tactics used by males (DeBock 1970; Geist 1964). In addition, male–male competition is known to be very dangerous in mountain goats because of their sharp horns that can injure or kill conspecifics (Geist 1967). On the other hand, there is very little information on the rut of mountain goats (Côté and Festa-Bianchet 2003). For example, it is not known whether females mate with >1 male as observed in other ungulates (Coltman et al. 1999; Hogg and Forbes 1997) and what characteristics of males affect access to estrous females (Côté and Festa-Bianchet 2003). Because both reproductive success and the ability to provide maternal care increase with age in female mountain goats (Côté and Festa-Bianchet 2001a, 2001b) and most females breed within <2 weeks according to the clumped distribution of birth dates of young (Côté and Festa-Bianchet 2001c), males may benefit by selectively tending females that are likely to have a higher reproductive value when possible (Fawcett and Johnstone 2003). This is especially true for mountain goats, because males can only defend 1 female at a time (Geist 1964).

Our main objective was to determine the influence of the age and social rank of males on the formation of consort pairs with estrous females (i.e., tending) in mountain goats, using data collected in a marked population over 3 ruts. In addition, to better document the mating system of this alpine ungulate, we quantified the behaviors performed by males and females in consort pairs, the use of alternative mating tactics by competing males, and dates when matings occurred. Finally, we also assessed whether males showed mating preferences according to their age and social rank. Interestingly, it was possible to test this hypothesis because potential mate selection by males occurred in our study population because of the variability in the capacity of females to produce offspring, and individual variations in experience and social status of competing males (Fawcett and Johnstone 2003). We predicted that old and dominant males would tend a higher number of estrous females when compared to young and subordinate males, and also would form consort pairs more often with prime-aged and old females than with young females to potentially increase their reproductive success.

Materials and Methods

Study area and population.—We observed mountain goats from early November to early December 2004–2006 at Caw Ridge (54°N, 119°W), in the Front Range of the Rocky Mountains in west-central Alberta, Canada. The population of native mountain goats at Caw Ridge uses about 28 km^2 of alpine tundra, including short cliffs and open forest at 1,750–2,170 m in elevation. This population has been intensively studied since 1989 and since 1993 >98% of individuals aged ≥1 year have been recognizable through combinations of unique ear tags or neck collars. Côté et al. (1998) provide details about capture and marking techniques for our study population. The long-term research project at Caw Ridge and the present study were approved by the Animal Care Committee of Université Laval, affiliated with the Canadian Council for Animal Care, and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Although the population was marked, we observed 3–5 immigrant males in each rut that were not seen during the previous and following summers in the Caw Ridge population, indicating that they came specifically for the rut and left afterward.

Behavioral observations.—We used spotting scopes (15–45×) to identify goats and members of consort pairs at distances ranging from 200 to 700 m. We recorded 17 consort pairs in 2004, 34 in 2005, and 21 in 2006. Sixty-three (87.5%, $n = 72$) of these consort pairs included 2 marked individuals, whereas the other pairs observed were composed of an immigrant adult (≥3-year-old) male of unknown age and a marked female from the study population. When topography allowed, we conducted focal observations (Altmann 1974) on both the estrous female and the male tending her. A female was considered in estrus, which is thought to last about 2 days in mountain goats (DeBock 1970; Geist 1964), when at least 1 male performed courtship behaviors and constantly followed her. Behaviors (Table 1) of each member of the consort pair were then recorded every minute. Every 2 min, the distance between the female and the tending male was visually estimated in meters by previously trained observers, and each member of the pair was classified as either motionless, approaching, or moving away from the other to determine who was responsible for the maintenance of the consortship.

TABLE 1.—Description and percentage of time spent (mean ± *SE*) in different behaviors by adult (≥3-year-old) male and female mountain goats (*Oreamnos americanus*) observed in consort pairs ($n = 34$) during the ruts 2004–2006 at Caw Ridge, Alberta, Canada.

Behavioral categories	Description	Female (%)	Male (%)
Nonsexual		99.8	89.9
Forage	Either grazing or browsing	40.0 ± 4.4	7.4 ± 2.2
Rest	Resting	16.0 ± 3.9	15.7 ± 3.6
Alert	Standing, head upright with raised ears	0.3 ± 0.1	0.8 ± 0.6
Stand	Standing without being alert	30.5 ± 3.8	53.4 ± 3.4
Locomotion	Either walking or running	9.8 ± 1.3	7.3 ± 0.8
Others	Scratching, urinating, or defecating	3.0 ± 0.7	2.1 ± 0.5
Male−male interaction	Interaction between 2 males aged ≥1 year	—	1.8 ± 0.4
Male−female interaction	Nonsexual agonistic interaction between a male and a female	0.1 ± 0.0	0.0 ± 0.0
Female−female interaction	Interaction between 2 females aged ≥1 year	0.1 ± 0.0	—
Pitting behavior	Throwing dirt and snow with foreleg to flank while sitting	—	0.9 ± 0.3
Bush rubbing	Marking grasses with occipital gland located at the base of the horns	—	0.5 ± 0.2
Courtship[a]		0.2	10.1
Low stretch	Submissive approach of a male toward a female	—	0.1 ± 0.1
Tongue flicking	Tongue flicking in and out of the mouth when near a female	—	1.9 ± 0.4
Pawing a recumbent female	Front leg kick along a resting female's flank	—	0.4 ± 0.2
Pursuit	Pursuing female	—	0.5 ± 0.3
Sexual investigation	Investigation of female's genitalia	—	2.5 ± 0.3
Lip curl or flehmen	Upper lip is pulled back sharply after nuzzling female's genitalia or urine	—	1.5 ± 0.4
Foreleg kick	Front leg kick between or along female's haunches	—	1.2 ± 0.3
Chin resting	Male deposes his chin on female's back	—	0.3 ± 0.1
Mounting attempt	Mounting female without copulation	—	1.5 ± 0.5
Mating	Copulation	0.2 ± 0.1	0.2 ± 0.1

[a] For a detailed description of courtship behaviors, see Geist (1964) and DeBock (1970).

Focal observations also allowed us to monitor the use of alternative mating tactics and any replacement of the tending male. When a tending male was replaced by another male (i.e., a takeover), we began a new focal observation. We noted the duration of copulations and whether a copulation was terminated by the male or the female. The male was considered to have terminated the copulation when the female remained in a standing position and near the male after the copulation. Matings that occurred outside focal observations also were noted opportunistically. Focal observations were conducted as long as goats were in sight and those lasting <30 min were discarded. Altogether, a total of 34 focal observations over the 3 ruts were conducted and lasted on average 79 min ± 8 *SE*. In 18% ($n = 34$) of the focal observations, an unmarked male was tending the estrous female.

Social dominance.—During the rut, we recorded agonistic interactions between adult males using all-occurrences sampling (Altmann 1974). We also recorded agonistic interactions during focal observations. Agonistic interactions usually included a "present threat," a posture that enhances apparent size by arching the back (Chadwick 1977; Geist 1964) while approaching the opponent. We defined an interaction resolved when 1 of the opponents withdrew by moving away from the approaching opponent, often at a quick pace. On a few occasions ($n = 7$ of 440 agonistic interactions recorded over the 3 years), agonistic encounters escalated into a circle fight (Chadwick 1977), where 1 or both males were injured (i.e., bleeding), twice due to horn jabs from the opponent. After such fights, the goat that lost was always chased away by the winner.

Data analysis.—To determine which sex was responsible for the maintenance of the consort pair, we used a generalized linear mixed model (GLMM) to examine if the proportion of time 1 member was approaching or moving away from the other, fitted as the dependent variable, was sex-biased. Proportions were arcsine–square-root transformed to approximate a normal distribution. Identity of mountain goats observed in consort pairs was fitted as a random term in the GLMM to control for multiple observations of the same individual over time (Littell et al. 1998). The significance of individual effects was tested by comparing the log likelihood of models with and without the random term (Steele and Hogg 2003). Because the random term did not explain significant variance in the model, we present a generalized linear model (GLM) rather than a GLMM.

To determine social rank, we ordered adult males in annual hierarchies following the methodology of de Vries (1998), using MATMAN 1.0 for Windows (Noldus Information Technology 1998). We included in the matrix only males with a minimum of 3 observed dyadic relationships. We 1st calculated the linearity of dominance hierarchies each year with the index h' (de Vries 1995), modified from Landau's linearity index h (Landau 1951), to take into account unknown relationships. The index h' varies from 0 (no linearity) to 1 (perfect linearity). To determine if h' was statistically

Table 2.—Dominance matrices of rutting adult (≥3-year-old) male mountain goats (*Oreamnos americanus*) in November and December 2004–2006 at Caw Ridge, Alberta, Canada.

Year	No. males	Interactions observed	% of dyads observed	h'[a]	P[b]	DC[c]
2004	10	54	53.3	0.52	0.09	1.00
2005	21	276	51.4	0.43	<0.001	1.00
2006	16	80	43.3	0.36	0.03	1.00

[a] Linearity index (see "Materials and Methods").
[b] *P*-value associated with the linearity test using the h' index, based on 10,000 randomizations (de Vries 1998).
[c] Directional consistency index in encounter outcomes (see "Materials and Methods").

significant, a sampling process using 10,000 randomizations was performed to compare matrices (de Vries 1995). If significantly linear, the dominance hierarchy was reorganized by an iterative procedure (1,000 sequential trials) to minimize inconsistencies (Côté 2000; de Vries 1998). Although the dominance hierarchy of 2004 was not quite significantly linear (Table 2), we ranked individuals with the iterative procedure because h' was higher in that year than in other years and there was no inconsistency in any matrix in any year (Table 2; Gendreau et al. 2005). Because males aged ≥6 years always won against individuals aged 3–4 years based on 137 observed encounters, but interacted with them less often than with older males, we assigned dominance to the older individual in all unknown relationships between these 2 age classes before ordering individuals in a dominance hierarchy (see Côté [2000] for details). Because matrix size varied among years, we transformed social ranks as 1 − (rank/N_i), where N_i is the number of adult males in the matrix in year i (Côté 2000). Standardized social ranks (hereafter referred as social rank) ranged from 0 (subordinate) to 1 (dominant). Each year, we also calculated the directional consistency index, which varies from 0 (the outcome of interactions within a dyad is unpredictable) to 1 (complete predictability in the outcome of an encounter based on earlier interactions—van Hooff and Wensing 1987). We then tested for a relationship between social rank and age in adult males using a GLMM with identity of males fitted as a random term. The quadratic term of age (age^2) was fitted as an additional effect to test for a possible curvilinear relationship between rank and age. We also used a GLMM to test if social ranks of males observed in at least 1 consort pair were higher than those of adult males never observed in consort.

To investigate whether older and dominant males tended prime-aged and older females more often than younger females, we used a GLMM with age of females as the dependent variable, and age and social rank of males as independent variables. Identity of males was fitted as a random term. To meet parametric test assumptions, age of females was log-transformed before the GLMM analysis. Because the random term did not explain any variance in the model, we present a GLM instead of a GLMM. As the total number of young produced was known for each female (see Côté and Festa-Bianchet [2001a, 2001c] for details), we also used this variable as an index of fecundity in a GLM, because the random term female identity was not significant. However, because the number of young produced was highly dependent on age of the female (GLMM with identity of females fitted as a random term: $F = 132.0$, $d.f. = 1, 15$, $P < 0.0001$, $n = 47$ observations of 31 females), we also used the residuals of the number of young produced on age as an index of female quality for production of young when assessing mate choice by males. Finally, we tested whether old females, which are also more experienced, mated earlier than younger ones, because parturition date has been reported to decrease with increasing age in some female ungulates (Festa-Bianchet 1988; Mitchell and Lincoln 1973), although no such relationship has been previously found for mountain goats in our study population (Côté and Festa-Bianchet 2001c).

All analyses were performed in SAS version 9.1 (SAS Institute Inc. 2003). Statistical tests were 2-tailed and significance levels were set at 0.05. Inspection of residuals indicated no violation of assumptions of normality and homoscedasticity. Means ± *SE* are presented.

Results

Age of males and tending.—In all 63 consort pairs of known-age individuals observed over the 3 ruts, males were always ≥4 years of age. Although males ≥6 years represented only 27–38% of males aged ≥1 year in our study population, they were involved in 89% of consort pairs. This indicated that male mountain goats must reach at least 4 years of age to successfully tend an estrous female, but were more likely to be successful from 6 years of age onward. On average, age of males in consort pairs was 7.3 ± 0.2 years ($n = 20$ individual males), whereas that of tended females was 7.4 ± 0.4 years (range: 3–16 years, $n = 31$ individual females).

Social rank of males and tending.—Dominance hierarchies in adult male mountain goats were nearly linear in all years and the outcomes of encounters within each dyad were always consistent with the results of previous interactions in the same dyad that year (Table 2). Social rank was strongly related to age ($F = 25.4$, $d.f. = 1, 18$, $P < 0.0001$, $n = 47$ observations from 27 individuals) and age^2 ($F = 13.3$, $d.f. = 1, 18$, $P = 0.0018$; Fig. 1). Adult males that formed consort pairs with estrous females had a higher social rank (0.61 ± 0.05; $n = 28$) than those that were not observed tending females (0.25 ± 0.04, $n = 19$; $F = 12.8$, $d.f. = 1, 19$, $P = 0.002$; Fig. 2). Seventy-nine percent of the males observed in consort pairs had a high rank for their age (i.e., positive residuals of rank on age; $n = 59$ consort pairs with a male of known social rank). Most males observed in consort pairs (86%, $n = 59$) also were in the top half of the dominance hierarchy (i.e., social rank > 0.50; numbers according to rank in Fig. 3a). During focal observations, takeovers occurred in 12% of the consort pairs and the challenging male was always dominant over the male that he replaced (J. Mainguy et al., in litt.).

Behaviors of tending males and estrous females.—Although females and males in consort pairs spent similar amounts of time resting and moving, their time budgets differed greatly

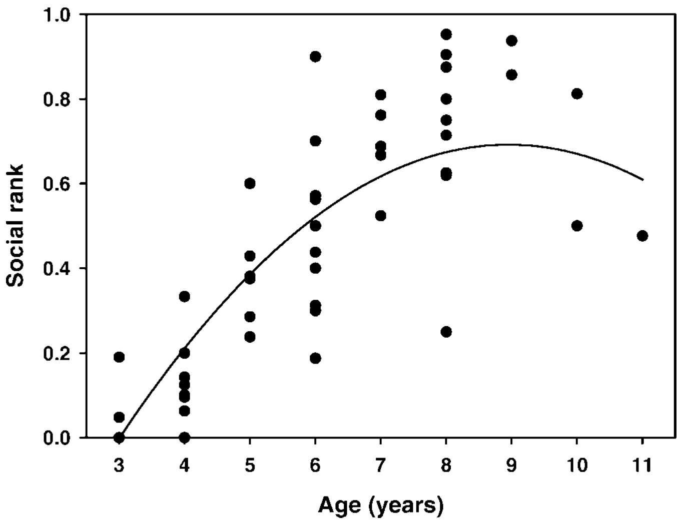

FIG. 1.—Relationship between age and social rank, which varies from 0 (subordinate) to 1 (dominant), in adult (≥3-year-old) male mountain goats (*Oreamnos americanus*) during the ruts 2004–2006 at Caw Ridge, Alberta, Canada.

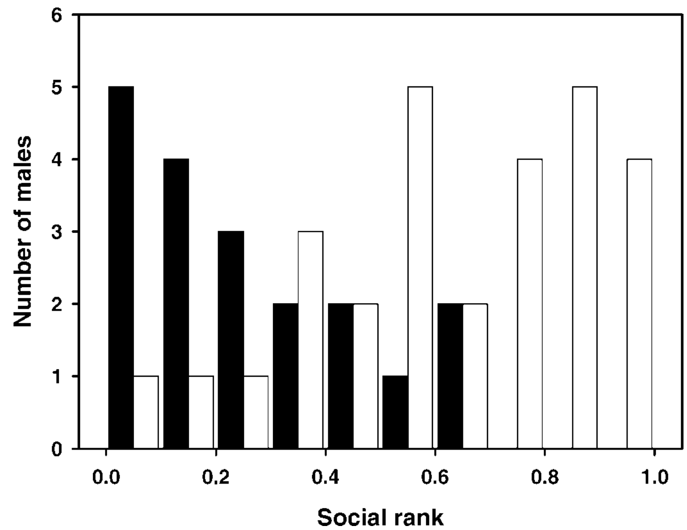

FIG. 2.—Frequency distribution of adult (≥3-year-old) male mountain goats (*Oreamnos americanus*) that were observed (empty bars; $n = 28$) or not (filled bars; $n = 19$) in at least 1 consort pair with an estrous female according to their social rank, which varies from 0 (subordinate) to 1 (dominant), during the ruts 2004–2006 at Caw Ridge, Alberta, Canada.

(Table 1). Females mainly foraged, whereas males spent little time foraging (>5-fold difference; Table 1). In addition, males were observed more than one-half of the time standing near females, whereas females were observed standing for approximately one-third of the time (Table 1). Thus, both sexes were often motionless (i.e., not moving away from or closer to each other; females: 88.0% ± 1.5%; males: 87.4% ± 1.2% at 2-min intervals during focal observations) and the mean distance between a tending male and an estrous female was 4.7 ± 0.4 m. Males approached the estrous female (9.4% ± 1.2%) more often than the opposite (1.5% ± 0.4%; $F = 45.0$, *d.f.* = 1, 66, $P < 0.0001$) and thus, females were moving away from the tending male (10.4% ± 1.3%) more often than males moved away from females (3.2% ± 0.5%; $F = 19.7$, *d.f.* = 1, 66, $P < 0.0001$). On many occasions, males moved away to defend the female against other males (about 2% of their time; Table 1) or to investigate another nearby female. Of all courtship behaviors by tending males recorded during focal observations ($n = 281$), 26% ± 6% were directed toward a female other than the estrous focal female.

Mate choice by males.—Age of females observed in consort pairs tended to be positively correlated with social rank of males ($F = 3.88$, *d.f.* = 1, 57, $P = 0.0536$; Fig. 3a), but not with age of males when social rank was accounted for ($F = 0.67$, *d.f.* = 1, 56, $P = 0.42$). However, when using age-specific social rank of males (i.e., the residuals of social rank on age because the 2 variables were strongly related; Fig. 1) together with age as explanatory variables to try disentangling the effects of dominance from those of age, we found that age of females was positively related to age of males ($F = 4.61$, *d.f.* = 1, 61, $P = 0.0357$; Fig. 3b), but not to age-specific social rank ($F = 1.26$, *d.f.* = 1, 56, $P = 0.27$). When using the total number of young a female has produced so far in life instead of her age, we found the same positive relationship with age of males ($F = 5.70$, *d.f.* = 1, 61, $P = 0.0201$), but not with social rank ($F = 0.92$, *d.f.* = 1, 56, $P = 0.34$) or age-specific social rank ($F = 0.97$, *d.f.* = 1, 56, $P = 0.33$) once age of males had been accounted for in the model. When social rank was fitted alone, it was positively related with the total number of young produced by the tended female ($F = 4.34$, *d.f.* = 1, 57, $P = 0.0418$). However, males did not appear to discriminate among females that had produced more or fewer young for their age (i.e., the residuals of the number of young produced on age of females) according to their own age ($F = 1.10$, *d.f.* = 1, 61, $P = 0.30$), social rank ($F = 0.04$, *d.f.* = 1, 56, $P = 0.84$) or age-specific social rank ($F = 0.00$, *d.f.* = 1, 56, $P = 0.97$).

Reproductive tactics and matings.—In 6% of the consort pairs monitored through focal observations, we witnessed coursing by 1 or 2 subordinate males aged 4–6 years. No other alternative tactics such as blocking (sensu Hogg 1984) were observed. On only 1 occasion during focal observations did a coursing male mate with the focal estrous female. In contrast, 44% of tending males were observed mating with the focal female. Whether mating occurred in the other consort pairs outside the focal observation could not be determined. Other than during focal observations, 2 males gained matings through coursing for a total of 9% of all matings observed ($n = 32$ matings).

All matings observed, either through tending or coursing, occurred between 14 November and 2 December, and 94% of them occurred within a period of 10 days starting on 16 November (Fig. 4). However, the median date of mating varied among years (Kruskal–Wallis test, $H = 11.0$, *d.f.* = 2, $P = 0.004$) because in 2005 (median = 18 November) most matings were observed sooner than in 2004 (median = 22 November) or 2006 (median = 23 November). When accounting for year, mating date was not affected by age of females (GLMM with identity of females fitted as a random term: $F = 0.64$, *d.f.* = 1,

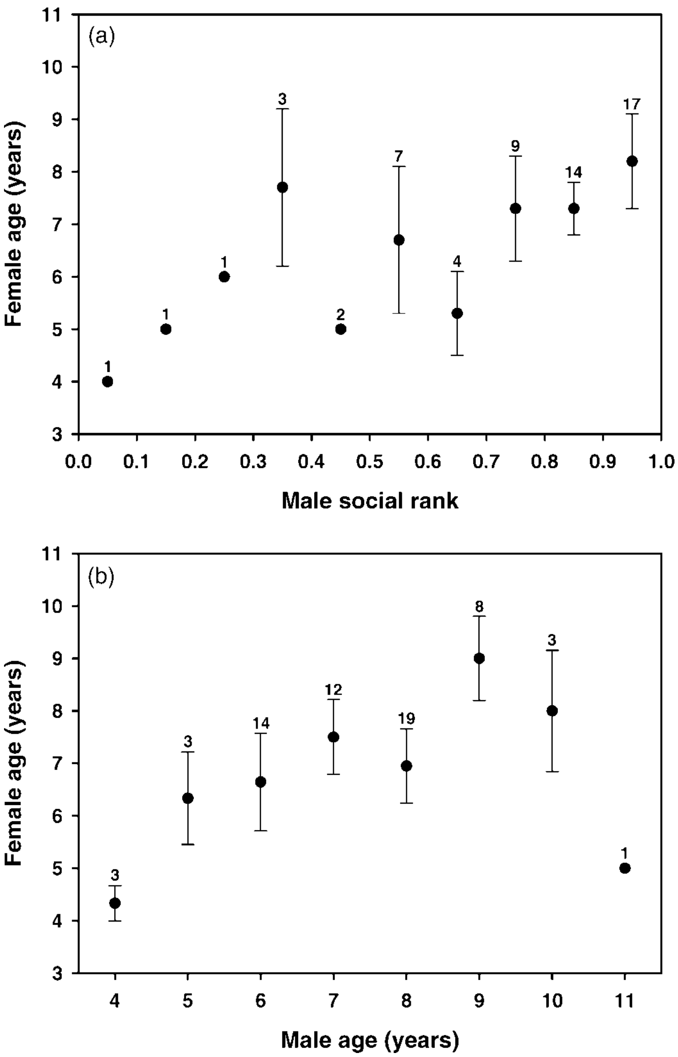

FIG. 3.—Relationships between age (mean ± *SE*) of female mountain goats (*Oreamnos americanus*) observed in consort pairs and a) social rank of males ($n = 59$), which varies from 0 (subordinate) to 1 (dominant), and b) age of males ($n = 63$), during the ruts 2004–2006 at Caw Ridge, Alberta, Canada. Sample sizes are indicated above error bars.

12, $P = 0.44$; Fig. 4), even after removing the 16-year-old female outlier (Fig. 4) that could have possibly mated in her 2nd estrous cycle. Among all matings observed, males were seen to copulate with the same female on average 3 ± 1 times (range: 1–10 times). Copulations lasted on average 3 s (range: 1–6 s) and 83% were terminated by the male. In 2005, 50% ($n = 14$) of the females mated with 2 different males, but we did not observe any female mated by >1 male in the other 2 years. All multiple matings observed between a female and different males occurred within 2 days. Of all individual females observed mating ($n = 24$ "female-years"), 17 (71%) gave birth the following spring out of a total of 84 births recorded (S. D. Côté, in litt.). We have thus witnessed about 20% of the matings that resulted in births of young (annual range: 14–29%), highlighting the difficulty of monitoring mating behavior in this alpine ungulate.

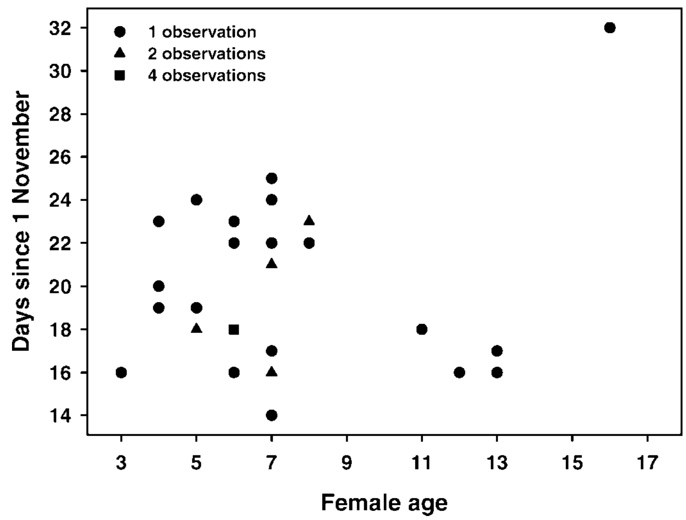

FIG. 4.—Mating date (1 November = 1) in relation to age of females ($n = 32$) in mountain goats (*Oreamnos americanus*) during the ruts 2004–2006 at Caw Ridge, Alberta, Canada. Multiple matings between a female and a male during the same day were considered as a single event.

DISCUSSION

Age and social rank were 2 important characteristics of males associated with the formation of consort pairs with estrous females in mountain goats, and both traits were positively related to each other until about 8 years of age. Because structural size and body mass increase with age until asymptotic mass and size are reached, and generally confer advantages during intrasexual combats (McElligott et al. 1998; Pelletier and Festa-Bianchet 2006; Wolff 1998), prime-aged (6- to 9-year-old) male mountain goats were thus mostly observed using the tending tactic, which is known to be the most rewarding in terms of reproductive success in polygynous ungulates, such as mountain goats, that can only defend a single female at a time (Coltman et al. 2002; Saunders et al. 2005). Males <4 years of age, despite representing 46–56% of the population segment composed of males at Caw Ridge and being sexually mature from 1 year of age (Henderson and O'Gara 1978), were never seen tending females or even coursing them during focal observations. This suggests that age at 1st reproduction in male mountain goats is likely late, possibly ≥5 years for most males according to focal observations and matings observed, when compared to other similar-sized polygynous ungulates. For instance, in feral goats (*Capra hircus*) and Soay sheep, males can participate actively in reproduction when only a few months old (Saunders et al. 2005; Stevenson and Bancroft 1995).

During the rut, male mountain goats face the risk of serious injuries from fights when approaching tending pairs because of aggressive retaliation by dominant males and dangerous horns (Geist 1967). Therefore, when a male attempted coursing an estrous female momentarily left unattended, he always withdrew when the dominant male returned (J. Mainguy et al., in litt.), suggesting the existence of a preestablished dominance hierarchy among males. This was indicated by strongly linear social hierarchies, which can reduce the energy costs and risks of fight injuries (Maynard Smith 1974; McElligott et al. 1998). Although reversals in dyadic relationships can sometimes occur within the same rutting season (e.g., DeYoung et al. 2006), this was not observed in our study population. Males that used coursing were thus always ranked lower in the dominance hierarchy than tending males, but could be observed to form consort pairs with estrous females on other occasions when higher-ranking males were absent (J. Mainguy et al., in litt.). This suggests that a male could adopt 1 tactic or the other depending on the social rank of the other males present in a group and the number of females in estrus (Hogg and Forbes 1997). Furthermore, 37% of the consort pairs ($n = 59$) included 1 of the 2 highest-ranking males for each rut, clearly indicating the advantage of attaining a high social rank to gain mating success and, ultimately, greater chances of obtaining success of paternity.

Males that used the tending tactic, not surprisingly, were responsible for the maintenance of the consortship with the estrous female, as observed in other ungulates (e.g., Berger 1989; Hogg 1984). In consort pairs, females did not exhibit any apparent sexual behavior except mating, whereas males spent one-tenth of their time in courtship behaviors, mainly testing receptivity of females. In contrast to females, male mountain goats fed very little during the rut, a common pattern reported in male ungulates (Miquelle 1990; Pelletier 2005). Despite these differences, both females and males spent much of their time standing. This is in sharp contrast with time budgets in summer when both sexes mainly forage and rest (Côté and Festa-Bianchet 2003; Mainguy and Côté 2008). By spending a large amount of time standing in proximity of the tended female, a male may protect her against rivals and better detect the approach of higher-ranking competitors. Standing can thus be regarded as part of an ''active'' behavior, as previously suggested by Mahers and Byers (1987) in rutting male bison.

One of our most interesting findings was that old and dominant male mountain goats were more likely to tend experienced females than young females. Exhibiting mating preferences for prime-aged and old females that are more likely to produce young could thus be part of a strategy to increase reproductive success in males in polygynous ungulates. Support for this hypothesis comes from a study on fallow deer (*Dama dama*) by Say et al. (2003), who have shown that males that mated with young females achieved a lower reproductive success than those that mated with older females, although they did not specifically discuss whether mate choice by males occurred in this species. In mountain goats, prime-aged and old females produce more young than younger females, at least until 10 years of age (Côté and Festa-Bianchet 2001a). In addition, prime-aged and old female mountain goats produce more sons than do young females (Côté and Festa-Bianchet 2001b). Sons are normally more costly to rear in sexually dimorphic and polygynous species (Bérubé et al. 1996), indicating that the ability to provide maternal care likely increases with female age. Competitive male mountain goats could thus theoretically benefit from tending prime-aged and old females. Similar to our findings, Preston et al. (2005) reported that competitive male Soay sheep focused their mating activity toward heavier females that normally exhibit higher reproductive success. In bison, Berger (1989) also reported that old males approached barren females more often than lactating and nulliparous females during the rut because barren females were more likely to give birth the following spring, supporting an apparent evaluation of the reproductive potential of females by males. However, even if all reproductively active males should attempt tending females of high reproductive value, only high-quality males such as dominant ones should be successful in tending high-quality females, especially in presence of competitors (Fawcett and Johnstone 2003). Therefore, our results suggest that mate choice by males occurs in mountain goats, but appears to be mostly performed by dominant males.

Although the mechanisms leading to the formation of consort pairs and the exhibition of mating preferences remain to be clearly identified, they could be partly based on physiological cues such as odoriferous compounds associated with fertility (e.g., estrogen) that are found in females' urine or feces (Gesquiere et al. 2007). In ungulates, the vomeronasal organ, which is used by males during flehmen (Table 1), could possibly play a role in mate choice and the expression of mating behaviors (Ungerfeld et al. 2006). Male mountain goats observed in consort pairs spent about 4% of their time scenting the urine or genitalia of the tended female or of other nearby females. Although speculative, it is possible that males may not only detect if females are in estrus when performing flehmen, but also potentially select among them. However, it is important to note that females also may exert mating preferences, because they are generally regarded as the choosy sex (Andersson and Simmons 2006). For example, female mountain goats could actively avoid mating with low-quality males or delay breeding when they are in presence of young males only (e.g., Holand et al. 2006; Komers et al. 1999; Mysterud et al. 2002). Mate choice is thus more likely the result of preferences by both males and females, but much remains to be done to understand the underlying mechanisms (Andersson and Simmons 2006).

Our study revealed new insights on the reproductive ecology of mountain goats. We showed that males used alternative mating tactics as reported in some species of wild sheep (Coltman et al. 1999; Hogg 1984), which could lead to sperm competition (Hogg and Forbes 1997; Preston et al. 2003), as the result of multiple matings between a female and different tending and coursing males. However, the potential for sperm competition in mountain goats is likely lower than in wild sheep because they have much smaller testes than sheep for their body size (J. Mainguy et al., in litt.; Møller 1989). Because all multiple matings occurred within 2 days for the same female, our results also support earlier observations by Geist (1964) and DeBock (1970), who suggested that estrous lasted about 2 days in mountain goats. In addition, because both males and females can mate with >1 partner during each rut, the mating system of mountain goats perhaps can be better described as a polygamous (or promiscuous) rather than a purely polygynous mating system, similarly to other ungulates such as Soay sheep (Coltman et al. 1999). The clumped temporal distribution of matings in November was similar to that of birth dates of young in May, where 80% of all births occurred within 2 weeks (Côté and Festa-Bianchet 2001c). This suggests that gestation length in mountain goats exhibits low variability such as in other large temperate herbivores (Holand et al. 2006). Finally, age of females did not affect date of mating, which is in accordance with previous results of Côté and Festa-Bianchet (2001c), who reported no effect of maternal age on birth dates of young in the population at Caw Ridge.

Overall, we showed that both age and social rank were important determinants of mating success in male mountain goats, and provided the 1st detailed and quantitative information on the rut of this polygamous alpine ungulate. In addition, our results revealed that high-quality male ungulates could potentially maximize their fitness not only through the use of the most rewarding mating tactic, but also by showing mating preferences for females of high reproductive value.

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Literature Cited

Alberts, S. C., J. C. Buchan, and J. Altmann. 2006. Sexual selection in wild baboons: from mating opportunities to paternity success. Animal Behaviour 72:1177–1196.

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49:227–267.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, New Jersey.

Andersson, M., and L. W. Simmons. 2006. Sexual selection and mate choice. Trends in Ecology and Evolution 6:296–302.

Berger, J. 1989. Female reproductive potential and its apparent evaluation by male mammals. Journal of Mammalogy 70:347–358.

Bérubé, C. H., M. Festa-Bianchet, and J. T. Jorgenson. 1996. Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. Behavioral Ecology 7:60–68.

Bobek, B., K. Perzanowski, and J. Weiner. 1990. Energy expenditure for reproduction in male red deer. Journal of Mammalogy 71:230–232.

Chadwick, D. H. 1977. The influence of mountain goat social relationships on population size and distribution. Pp. 74–91 in Proceedings of the first international mountain goat symposium (W. Samuel and W. G. MacGregor, eds.). Province of British Columbia, Ministry of Recreation and Conservation, Fish and Wildlife Branch, Victoria, British Columbia, Canada.

Coltman, D. W., D. R. Bancroft, A. Robertson, J. A. Smith, T. H. Clutton-Brock, and J. M. Pemberton. 1999. Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. Molecular Ecology 8:1199–1209.

Coltman, D. W., M. Festa-Bianchet, J. T. Jorgenson, and C. Strobeck. 2002. Age-dependent sexual selection in bighorn rams. Proceedings of the Royal Society of London, B. Biological Sciences 269:165–172.

Côté, S. D. 2000. Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. Behaviour 137: 1541–1566.

Côté, S. D., and M. Festa-Bianchet. 2001a. Reproductive success in female mountain goats: the influence of age and social rank. Animal Behaviour 62:173–181.

Côté, S. D., and M. Festa-Bianchet. 2001b. Offspring sex ratio in relation to maternal age and social rank in mountain goats (*Oreamnos americanus*). Behavioral Ecology and Sociobiology 49:260–265.

Côté, S. D., and M. Festa-Bianchet. 2001c. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia 127:230–238.

Côté, S. D., and M. Festa-Bianchet. 2003. Mountain goat *Oreamnos americanus*. Pp. 1061–1075 in Wild mammals of North America: biology, management and conservation (G. A. Feldhamer, B. C. Thomson, and J. A. Chapman, eds.). John Hopkins University Press, Baltimore, Maryland.

Côté, S. D., M. Festa-Bianchet, and F. Fournier. 1998. Life-history effects of chemical immobilization and radiocollars on mountain goats. Journal of Wildlife Management 62:745–752.

DeBock, E. A. 1970. On the behavior of the mountain goat (*Oreamnos americanus*) in Kootenay National Park. M.S. thesis, University of Alberta, Edmonton, Alberta, Canada.

Deschner, T., M. Heistermann, K. Hodges, and C. Boesch. 2004. Female sexual swelling size, timing of ovulation, and male behaviour in wild West African chimpanzees. Hormones and Behavior 46:204–215.

Deutsch, C. J., M. P. Haley, and B. J. Le Boeuf. 1990. Reproductive effort of male northern elephant seals: estimates from mass loss. Canadian Journal of Zoology 68:2580–2593.

de Vries, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Animal Behaviour 50:1375–1389.

de Vries, H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Animal Behaviour 55:827–843.

DeYoung, R. W., S. Demarais, R. L. Honeycutt, K. L. Gee, and R. A. Gonzales. 2006. Social dominance and male breeding success in captive white-tailed deer. Wildlife Society Bulletin 34: 131–136.

Fabiani, A., F. Galimberti, S. Sanvito, and A. R. Hoelzel. 2004. Extreme polygyny among southern elephant seals on Sea Lion Island, Falkland Islands. Behavioral Ecology 15:961–969.

Fawcett, T. W., and R. A. Johnstone. 2003. Mate choice in the face of costly competition. Behavioral Ecology 14:771–779.

Festa-Bianchet, M. 1988. Age-specific reproduction of bighorn ewes in Alberta, Canada. Journal of Mammalogy 69:157–160.

Forsyth, D. M., R. P. Duncan, K. G. Tustin, and J.-M. Gaillard. 2005. A substantial energetic cost to male reproduction in a sexually dimorphic ungulate. Ecology 86:2154–2163.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Geist, V. 1964. On the rutting behavior of the mountain goat. Journal of Mammalogy 45:551–568.

Geist, V. 1967. On fighting injuries and dermal shields of mountain goats. Journal of Wildlife Management 31:192–194.

Gendreau, Y., S. D. Côté, and M. Festa-Bianchet. 2005. Maternal effects on post-weaning physical and social development in juvenile mountain goats (*Oreamnos americanus*). Behavioral Ecology and Sociobiology 58:237–246.

Gesquiere, L. R., E. O. Wango, S. C. Alberts, and J. Altmann. 2007. Mechanisms of sexual selection: sexual swellings and estrogen concentrations as fertility indicators and cues for male consort decisions in wild baboons. Hormones and Behavior 51:114–125.

Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology and Evolution 11:92–98.

Haley, M. P., C. J. Deutsch, and B. J. Le Boeuf. 1994. Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. Animal Behaviour 48:1249–1260.

Henderson, R. E., and B. W. O'Gara. 1978. Testicular development of the mountain goat. Journal of Wildlife Management 42: 921–922.

Hirotani, A. 1994. Dominance rank, copulatory behaviour and estimated reproductive success in male reindeer. Animal Behaviour 48:929–936.

Hogg, J. T. 1984. Mating in bighorn sheep: multiple creative male strategies. Science 225:526–529.

Hogg, J. T., and S. H. Forbes. 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk 'unconventional' tactic. Behavioral Ecology and Sociobiology 41:33–48.

Holand, Ø., et al. 2006. Adaptive adjustment of offspring sex ratio and maternal reproductive effort in an iteroparous mammal. Proceedings of the Royal Society of London, B. Biological Sciences 273:293–299.

Komers, P. E., B. Birgersson, and K. Ekvall. 1999. Timing of estrus in fallow deer is adjusted to the age of available mates. American Naturalist 153:431–436.

Landau, H. G. 1951. On dominance relations and the structure of animal societies: I. Effect of inherent characteristics. Bulletin of Mathematical Biophysics 13:1–19.

Le Boeuf, B. J. 1974. Male–male competition and reproductive success in elephant seals. American Zoologist 14:163–176.

Lidgard, D. C., D. J. Boness, W. D. Bowen, and J. I. McMillan. 2005. State-dependent male mating tactics in the grey seal: the importance of body size. Behavioral Ecology 16:541–549.

Littell, R. C., P. R. Henry, and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. Journal of Animal Science 76:1216–1231.

Mahers, C. R., and J. A. Byers. 1987. Age-related changes in reproductive effort of male bison. Behavioral Ecology and Sociobiology 21:91–96.

Mainguy, J., and S. D. Côté. 2008. Age- and state-dependent reproductive effort in male mountain goats, *Oreamnos americanus*. Behavioral Ecology and Sociobiology 62:935–943.

Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. Journal of Theoretical Biology 47:209–221.

McElligott, A. G., V. Mattiangeli, S. Mattiello, M. Verga, C. A. Reynolds, and T. J. Hayden. 1998. Fighting tactics of fallow bucks (*Dama dama*, Cervidae): reducing the risks of serious conflict. Ethology 104:789–803.

McElligott, A. G., F. Naulty, W. V. Clarke, and T. J. Hayden. 2003. The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? Evolutionary Ecology Research 5:1239–1250.

Miquelle, D. G. 1990. Why don't bull moose eat during the rut? Behavioral Ecology and Sociobiology 27:145–151.

Mitchell, B., and G. A. Lincoln. 1973. Conception dates in relation to age and condition in two populations of red deer in Scotland. Journal of Zoology (London) 171:141–152.

Møller, A. P. 1989. Ejaculate quality, testes size and sperm production in mammals. Functional Ecology 3:91–96.

Mysterud, A., T. Coulson, and N. C. Stenseth. 2002. The role of males in the dynamics of ungulate populations. Journal of Animal Ecology 71:907–915.

Mysterud, A., E. J. Solberg, and N. G. Yoccoz. 2005. Ageing and reproductive effort in male moose under variable levels of intrasexual competition. Journal of Animal Ecology 74:742–754.

Noldus Information Technology. 1998. MATMAN reference manual. Version 1.0 for Windows. Noldus Information Technology, Wageningen, The Netherlands.

Parga, J. A. 2006. Male mate choice in *Lemur catta*. International Journal of Primatology 27:107–131.

Peek, J. M., V. van Ballenberghe, and D. G. Miquelle. 1986. Intensity of interactions between rutting bull moose in central Alaska. Journal of Mammalogy 67:423–426.

Pelletier, F. 2005. Foraging time of rutting bighorn rams varies with individual behavior, not mating tactic. Behavioral Ecology 16: 280–285.

Pelletier, F., and M. Festa-Bianchet. 2006. Sexual selection and social rank in bighorn rams. Animal Behaviour 71:649–655.

Preston, B. T., I. R. Stevenson, J. M. Pemberton, D. W. Coltman, and K. Wilson. 2003. Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. Proceedings of the Royal Society of London, B. Biological Sciences 270:633–640.

Preston, B. T., I. R. Stevenson, J. M. Pemberton, D. W. Coltman, and K. Wilson. 2005. Male mate choice influences female promiscuity in Soay sheep. Proceedings of the Royal Society of London, B. Biological Sciences 272:365–373.

SAS Institute Inc. 2003. SAS/STAT user's guide. Release 9.1. SAS Institute Inc., Cary, North Carolina.

Saunders, F. C., A. G. McElligott, K. Safi, and T. J. Hayden. 2005. Mating tactics of male feral goats (*Capra hircus*): risks and benefits. Acta Ethologica 8:103–110.

Say, L., F. Naulty, and T. J. Hayden. 2003. Genetic and behavioural estimates of reproductive skew in male fallow deer. Molecular Ecology 12:2793–2800.

Setchell, J. M., and E. J. Wickings. 2006. Mate choice in male mandrills (*Mandrillus sphinx*). Ethology 112:91–99.

Steele, B. M., and J. T. Hogg. 2003. Measuring individual quality in conservation and behavior. Pp. 243–269 in Animal behavior and wildlife conservation (M. Festa-Bianchet and M. Apollonio, eds.). Island Press, Washington, D.C.

Stevenson, I. R., and D. R. Bancroft. 1995. Fluctuating trade-offs favour precocial maturity in male Soay sheep. Proceedings of the Royal Society of London, B. Biological Sciences 262:267–275.

Ungerfeld, R., M. A. Ramos, and R. Möller. 2006. Role of the vomeronasal organ on ram's courtship and mating behaviour, and on mate choice among oestrous ewes. Applied Animal Behaviour Science 99:248–252.

van Hooff, J. A. R. A. M., and J. A. B. Wensing. 1987. Dominance and its behavioral measures in a captive wolf pack. Pp. 219–252 in Man and wolf (H. W. Frank, ed.). Junk Publishers, Dordrecht, The Netherlands.

Wolff, J. O. 1998. Breeding strategies, mate choice, and reproductive success in American bison. Oikos 83:529–544.

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