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

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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 on average 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

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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 1996), 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 Wikking 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 1964). In addition, male–male competition is known to be very dangerous in mountain goats 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 km² 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.
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
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 $\geq 6$ 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 $1 - (\text{rank}/N_i)$, 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 ($\text{age}^2$) 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 Festan-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 Festan-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 $\pm$ 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 $\geq 4$ years of age. Although males $\geq 6$ years represented only 27–38% of males aged $\geq 1$ 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 $\pm$ 0.2 years ($n = 20$ individual males), whereas that of tended females was 7.4 $\pm$ 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 ($0.61 \pm 0.05; n = 28$) than those that were not observed tending females ($0.25 \pm 0.04; n = 19; F = 12.8, d.f. = 1, 19, P = 0.002; Fig. 2$). 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

<table>
<thead>
<tr>
<th>Year</th>
<th>No. males</th>
<th>Interactions observed</th>
<th>% of dyads observed</th>
<th>$h'$</th>
<th>$P^b$</th>
<th>DC$^c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td>10</td>
<td>54</td>
<td>53.3</td>
<td>0.52</td>
<td>0.09</td>
<td>1.00</td>
</tr>
<tr>
<td>2005</td>
<td>21</td>
<td>276</td>
<td>51.4</td>
<td>0.43</td>
<td>&lt;0.001</td>
<td>1.00</td>
</tr>
<tr>
<td>2006</td>
<td>16</td>
<td>80</td>
<td>43.3</td>
<td>0.36</td>
<td>0.03</td>
<td>1.00</td>
</tr>
</tbody>
</table>

$^a$ 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”).
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, df = 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, df = 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, df = 1, 57, P = 0.0536; Fig. 3a), but not with age of males when social rank was accounted for (F = 0.67, df = 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, df = 1, 61, P = 0.0357; Fig. 3b), but not to age-specific social rank (F = 1.26, df = 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, df = 1, 61, P = 0.0201), but not with social rank (F = 0.92, df = 1, 56, P = 0.34) or age-specific social rank (F = 0.97, df = 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 = 3.34, df = 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, df = 1, 61, P = 0.30). Thus, 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, df = 1, 61, P = 0.30). According to their social rank, which varies from 0 (subordinate) to 1 (dominant), during the ruts 2004–2006 at Caw Ridge, Alberta, Canada

Reproductive tactics and matings.—In 6% of the consort pairs monitored through focal observations, we witnessed courting 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 courting 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 courting for a total of 9% of all matings observed (n = 32 matings).

All matings observed, either through tending or courting, 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, df = 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, df = 1,
Among all matings observed, males were seen to copulate with the same female on average 3.61 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.

**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 courting 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 courting 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 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 reproducitively 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 (Gesquière 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 (Colman 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 courting 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, similar 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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