Social dominance and conflict reduction in rutting male Alpine ibex, *Capra ibex*

Christian S. Willisch[a,b] and Peter Neuhaus[a,c]
[a]Department of Eco-Ethology, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2009 Neuchâtel, Switzerland, [b]Zoological Museum, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland, and [c]Department of Biological Sciences, University of Calgary, 2500 University Dr. NW, Calgary AB, T2N 1N4, Canada

In polygynous ungulates, male mortality is thought to be linked to high-energy expenditures during the rut. However, Alpine ibex (*Capra ibex*) adult males show an unusually high survival during this time. Male Alpine ibex live in social groups and thus, we assumed that they might reduce energy-intensive interactions during the rut by establishing, early on, strict dominance hierarchies. To evaluate this hypothesis, we studied social interactions and mating behavior in a population of Alpine ibex in the Swiss Alps. In accordance with our prediction, and in contrast to other polygynous ungulates, male Alpine ibex decreased time spent in agonistic interactions and the number of fights during the rut compared with the prerut, irrespective of their age. Changes between access-holding males always occurred without foregoing fights and were entirely based on preestablished and stable dominance relationships. Therefore, dominant males always gained and held access to receptive females and thus managed to adopt the tending tactic. Subordinate males either left the consort pair or they adopted the coursing tactic in order to achieve temporary access to estrous females. They behaved extremely reluctantly toward dominants, as they never made use of overt aggression to challenge them or to create actively transient mating opportunities. Our study supports the hypothesis that costly intramale interactions are reduced during the mating season in Alpine ibex by the adherence to preestablished and stable dominance relationships. Accordingly, male Alpine ibex appear to be able to cut down on energy expenditures, which in turn, likely contributes to their superior survival. *Key words:* aggression, dominance, mating behavior, social system, survival, ungulate. *[Behav Ecol 21:372–380 (2010)]*

In polygynous ungulates, males normally invest much of their resources in the acquisition and defense of estrous females during the mating season (e.g., Yoccoz et al. 2002; McElligott et al. 2003; Mysterud et al. 2004, 2005; Pelletier 2005; Pelletier et al. 2006). Due to this, the body condition of males generally deteriorates considerably during the rut (Clutton-Brock et al. 1982; Forsyth et al. 2005), which, at the same time, increases the risks of dying during the subsequent winter (Stevenson and Bancroft 1995; Stevenson et al. 2004). Together, with strong reductions in food intake (e.g., Clutton-Brock et al. 1982; Miquelle 1990; Pelletier 2005; Willisch and Ingold 2007), the rut-related energy expenditures are, therefore, thought to be largely responsible for the typically male-biased mortality pattern in polygynous ungulates (Toigo and Gaillard 2003).

A survival study by Toïgo et al. (2007), on marked Alpine ibex (*Capra ibex*) in a population in the French Alps, recently indicated that male-biased adult mortality in this species is not as pronounced as their high degree of sexual dimorphism suggests. In fact, yearly survival of adult males, up to the age of 10–13 years, was exceptionally high (85–98%). Consequently, male survival did not only equal, under good conditions, survival of females, but also exceeded survival of other male ungulates by 5–20% (Toïgo et al. 2007), giving rise to the assumption that adult male Alpine ibex pursue an energetically conservative reproductive strategy during the rut.

In agreement with this supposition, the recent study of Willisch and Neuhaus (2009) revealed that male Alpine ibex made use of a presumed low-cost tactic during the rut. Because the tactic in question, termed "coursing," was mainly adopted by younger males, it was unlikely to contribute to the good survival of males >9 years of age. The authors, therefore, proposed another mutually not exclusive mechanism that might help to explain the good survival in adult male Alpine ibex. Particularly, they hypothesized that the males in this species might be able to save energy by reducing costly intramale interactions, which are ordinarily necessary to obtain or defend access to receptive females. Thus, normally, males of polygynous species are known to compete fiercely during the mating season to gain access to mating partners (e.g., Clutton-Brock and Albon 1979; Clutton-Brock et al. 1979; Fryxell 1987; Wells 1988; Apollonio et al. 1990; Alvarez 1993; Olsson 1993; McElligott et al. 1998; Wolff 1998; Hsu et al. 2005), which results in high energy expenditures and increased risks of mortality (Stevenson and Bancroft 1995; Stevenson et al. 2004). On the other hand, animals engaging not or less in such energy-consuming competitions might accordingly, considerably lower their energy expenditures, which in turn might contribute to an improved survival when compared with males of other species.

Although competition for access to receptive females, in polygynous ungulates, can generally be assumed to escalate (Parker 1974), examples exist in which animals refrain from taking part in escalating interactions (Hsu et al. 2005). Particularly, individuals that are likely to lose contests with supposedly stronger opponents should withdraw from agonistic interactions. Circumstances in which apparently inferior individuals are capitulating at an early stage of the interaction are typically occurring among animals of differing size/weight, fighting ability, or dominance rank (Hsu et al. 2005).

There are 2 main mechanisms for how inferior males can avoid fights that they are likely to lose. First, males may evaluate the actual fighting ability of their opponents each time they meet, either by assessing special physical traits (e.g., horn size: Hoem et al. 2007) or by ritualized assessment contests (e.g., vocalization and parallel walk: Clutton-Brock and Albon 1979; Bartos et al. 2007, but see Jennings et al. 2003). After having assessed an opponent, presumed weaker males can end interactions at an early stage without getting involved in serious fights. Second, males of socially living species might judge encounter situations based on the outcomes of earlier interactions with their opponents (Hsu et al. 2005; Taillon and Coté 2006). Thus, a male having lost an interaction encounter with another male in the past might avoid new, and above all, escalating interactions with the same male in the future. As a result, established dominance relationships could potentially replace long-lasting aggressive interactions among males, which would otherwise be necessary to clarify conflict situations (Jennings et al. 2006).

Because male Alpine ibex aggregate in social groups throughout the year (Villaret and Bon 1998), the existence of stable dominance relationships during the mating season is very likely (see, e.g., Pelletier and Festa-Bianchet 2006). If rutting male Alpine ibex would adhere to these relationships, also during competition for receptive females, they might be able to cut down on time- and energy-consuming intramale interactions. Hence, the establishment of dominance relationships and the strict adherence to them might make it unnecessary to engage in potentially escalating, agonistic interactions for access to receptive females during the rut.

Although many behavioral studies have pointed to the importance of dominance in male ungulates during the rut (Hogg 1987; Moore et al. 1995; Hogg and Forbes 1997; McElligott et al. 1998; Wolff 1998; Mainguy et al. 2008), including the Alpine ibex (Aeschbacher 1978; Willisch and Neuhaus 2009), no study has, to our knowledge, conclusively shown that obligatory dominance relationships may largely replace intensive agonistic interactions, such as assessment encounters and fights, to gain and maintain access to receptive females during the rut.

Based on the extraordinarily good survival detected in adult male Alpine ibex (Toïgo et al. 2007), and in line with the supposition of Willisch and Neuhaus (2009), we investigated, in this study, if adult male Alpine ibex were able to reduce energetically costly intramale competitions during the rut to attain access to receptive females by adhering to preestablished and stable dominance relationships. Particularly, we predicted that individual males should not have to engage in aggressive, potentially long-lasting, and costly physical interactions in order to gain access to receptive females. Instead, access should be entirely determined by preestablished dominance relationships among individual males during the rut. Furthermore, and in accordance with our hypothesis, we, expected costly intramale competition to be generally reduced during the rut compared with the prerut period, not only among young, and hence, not yet full-grown males, but also among older males, which are supposedly large enough to compete successfully for access to receptive females. Our study aimed to provide insights into how males of socially living ungulates may resolve conflicts over highly valuable resources without the necessity of escalating contests, and how the social system of animals may ultimately affect their energetics and survival.

MATERIALS AND METHODS

Study population

The study was carried out in the Alpine ibex population "Cape au Moine" (46°22′N; 07°09′E, 1700–2550 m), north of the village Les Diablerets, in the Swiss Alps. Population size varied between 220 and 270 animals. For a detailed description see Willisch and Neuhaus (2009). As reported for other populations (Villaret and Bon 1998), also at Cape au Moine, male Alpine ibex lived year round in a fission–fusion society where individuals were free to join or to leave a group (Conradt and Roper 2000). Some of the males were known to roam between this population and 2 adjacent populations. This behavior appeared to be expressed, particularly, before the onset of the rut in November/December (see also Parrini et al. 2003).

Mating system and mating tactics

In a recent study conducted in the same study area, Willisch and Neuhaus (2009) documented that single receptive females in the population were in association with an average of 4 and up to a maximum of 11 different males. Their observations furthermore revealed the existence of 2 alternative male mating tactics that are similar to the ones first described in male bighorn sheep (*Ovis canadensis*; Hogg 1984). A primary tactic termed "tending," in which individual males monopolized single receptive females by following and defending them persistently against competitors, and a secondary tactic termed "coursing," in which the remaining males tried to achieve temporary access to tended females by profiting from suddenly occurring mating opportunities when females started to run or when females moved or stood too far away from the tending male (Willisch and Neuhaus 2009). However, unlike coursing male bighorn sheep that typically initiate the so-called coursing chases themselves by physically attacking the tending male (Hogg 1984, 1987), coursing male Alpine ibex do normally wait rather opportunistically for the female first to move or run away from the tending male before engaging in her pursuit (Willisch and Neuhaus 2009). Overall, these observations indicate that Alpine ibex are polygynous ungulates that exhibit a high level of intramale competition for access to mating partners.

Sampling methods

Observations were conducted on individual male Alpine ibex between November and January in 2005–2006, 2006–2007, and 2007–2008 using spotting scopes (20–60 × 65/80). At the time of the study, up to 30 animals (20 males and 10 females) aged >1.5 years were individually marked using colored and numbered ear tags. Furthermore, based on morphological trait differences of the horns and the coat coloration, another 121 animals (101 males and 20 females) aged >2.5 years could individually be recognized in the study area. In the field, observers checked the identity of animals using a booklet containing pictures of all known individuals. In situations in which it was not possible to identify an animal, it was recorded as an unknown male or female. Whenever possible, observers took digital photographs of the animals and later checked their identities by comparing them with photographs of already described animals (Willisch and Neuhaus 2009). Regular crosschecking between observers, the subsequent analyses of photographs taken, as well as genetic identity analyses using up to 32 different microsatellite markers (Willisch 2009) of 13 animals sampled multiply (i.e., 10 males and 3 females; unpublished data) all indicated that the aforementioned identification method using booklets and photographs was sufficiently reliable.

The age of males was determined by counting the conspicuous annuli on the outer side of the horns (Ratti and Habermehl 1977). This was either done after capture or based on photographs taken from the free-ranging animals (for details see Willisch and Neuhaus 2009). Observations typically

covered all daylight hours. Distances between observers and animals varied, but ranged normally between 150 and 1500 m.

Continuous animal focal sampling (Altmann 1974) was used to obtain data on the proportion of time individual males spent in courtship and agonistic behaviors in the different observational periods (see below). Daily, up to 3 observers each selected between 1 and 3 focal animals and observed them continuously for as long as possible, resulting in 1141 hours of 238 continuous focal observations (4.8 ± 2.2 h, mean ± standard deviation) of a total of 71 different males. Observers tried to distribute observations equally over all individuals and age classes. To accomplish this, detailed accounts of all focal observations were kept and observers always decided, in advance, which individuals were to be chosen as focal animals each day. Courtship behaviors included mount, sniff, touch, lick, low stretch, tongue flick, masturbate, scent urinate, and flehmen performed toward females. Agonistic behaviors included evade, run away, displace, chase, rush, horn contact, horn clash, and intentional jump, mount performed toward males (for a detailed description of the behaviors see Willisch and Neuhaus 2009).

Furthermore, 208 females (47 in 2005–2006, 100 in 2006–2007, and 61 in 2007–2008), which were associated with at least 2 known males (1 tending and 1 coursing male) were scanned between 1–20 times a day to obtain data on associated males (ID, age) and their mating tactics (tending and coursing). Because all females could not be identified individually, an unknown portion may have been sampled multiply. Ad libitum sampling was used to record fights (i.e., physical interactions involving horn clashes) and other agonistic interactions between males, as well as changes in the access-defending and tending male.

Definition of dominance

In accordance with Drews (1993) we referred to dominance as an attribute of agonistic interactions between 2 individuals. Following the definition of De Vries (1998) we used the asymmetry information of wins and losses of the dyad members to determine their dominance relationships. Particularly, we called the individual of a dyad, which won more encounters than its opponent, "dominant." As a consequence the individual that won less often was considered to be "subordinate." A male was considered to be the winner of a single interaction encounter when it actively displaced or mounted its opponent. Conversely, a male was considered to be the loser when it evaded its opponent or when it was mounted by its opponent. Following fights, the winner was determined to be the male that followed its opponent persistently, occasionally displacing and hooking the loser with its horns.

Time budget data

To compare agonistic and courtship behaviors of males during the rut with the prerut, we determined different periods. Because copulations were brief and rare events, which were therefore hard to detect (Willisch and Neuhaus 2009), we defined the day when the first female was seen each year to be tended by a male as the beginning of the corresponding rutting period. These days were December 9, 5, and 13 in 2005, 2006, and 2007, respectively (Willisch and Neuhaus 2009). From these dates back- and onward, we split up the time between November and January into 6 biweekly periods with 2 prerut periods and 4 rutting periods each.

To check for changes in the proportion of time spent in courtship and agonistic behavior between different periods we calculated individual time budgets and performed restricted maximum likelihood mixed-effects models using the

"lme4" package in R (Crawley 2007). Because the agonistic and reproductive behavior of male Alpine ibex was likely to be age and/or size dependent, and asymptotic body size is normally not reached before the age of 8 years (Lüps et al. 2007), we also accounted for the factor, age, in these models. Animal ID, age of animals, and year of observation were entered as random factors (Pinheiro and Bates 2000). Proportions were arcsine square root transformed to meet normality (Zar 1999).

Fight data

To test for differences in the number of dyads whose males engaged in fights during the prerut and the rutting period, respectively, we first fitted generalized liner mixed-effects models with Poisson error distributions using the package lme4 in R (Crawley 2007). We considered the following variables: the response variable "number of dyads," a 2-level factor "fight" (fight or no fight), a 2-level factor "period" (prerut or rut), a 3-level factor "year" (2005–2007), and a continuous variable "observation effort" (number of observation days). The variables, fight and period, were fitted as fixed effects, whereas year and observation effort were included as random effects. Finally, to check whether the interaction term, fight × period, had a significant effect on the dependent variable (as suggested by our hypothesis), we compared models containing this interaction term with models omitting it (Crawley 2007).

Interaction data

For each dyad of 2 known males, we calculated: 1) the number of agonistic interactions won and lost by each animal (dominance situations); 2) the number of situations where a male arrived and took over the tending position from another male (takeover situations); 3) the number of situations where the tending male left apparently unforced and another, typically coursing, male started to tend the female (inheritance situations); and 4) the number of situations where 1 male adopted the coursing tactic next to the other tending male (tend–course situations). In order to obtain information on the directional consistency (DC) of dominance, takeover, inheritance and tend–course relationships between 2 specific males during the rut, we evaluated the proportion of dyads that were always won by the same male of the dyad using the DC index (see e.g., Pelletier and Festa-Bianchet 2006) implemented in the software package Matman 1.1 (Noldus; De Vries et al. 1993; De Vries 1998). The DC index can range between 0 (i.e., outcomes of interactions between dyad members are not predictable) and 1 (i.e., outcomes of interactions are always in favor of the same dyad members).

Binomial tests (Sheskin 2004) were used to check whether 1) takeovers indeed took place without preceding fights between 2 males, and 2) whether the overall winner (male which won more encounters) of a specific male dyad, determined by the dominance relationship, corresponded with the winner in the takeover (winner: access-gaining male), inheritance (winner: leaving male), and tend–course (winner: tending male) situations.

RESULTS

Courtship and agonistic behavior

The proportion of time allocated to courtship behaviors by males changed significantly between the observation periods; the main factor, age, and the interaction term, age × period, both had no significant effect (period: $F_{5,132} = 16.56$, $P = 0.0001$;
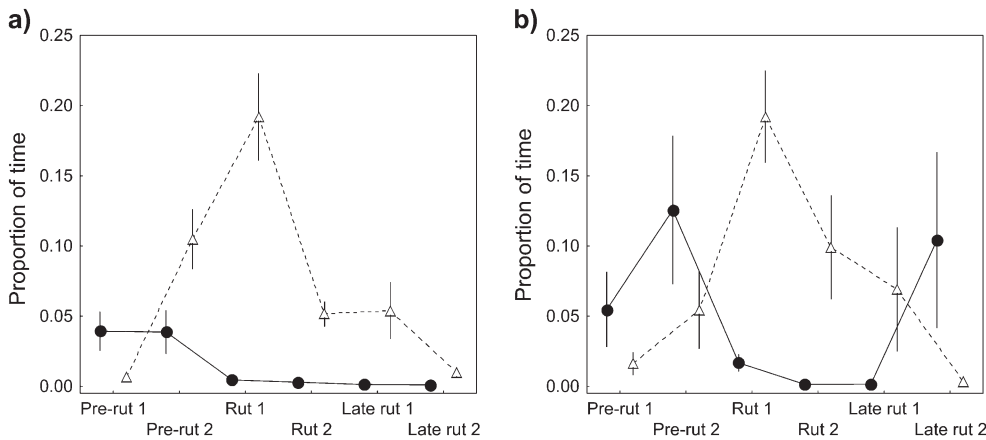
Figure 1
Mean (±standard error) proportion of time spent in courtship (open triangles, dashed line) and agonistic behaviors (filled circles, solid line) during the different observation periods by (a) males ≤8 years of age and (b) males ≥9 years of age.

age: $F_{1,29} = 0.22$, $P = 0.64$; and age × period: $F_{5,132} = 1.44$, $P = 0.21$). Hence, irrespective of the age of animals, male Alpine ibex increased the proportion of time spent in courtship behaviors from prerut to the rut. Peak level was reached during the first 2 weeks of the rut. Afterward, time allocated to courtship steadily declined to early prerut levels (Figure 1).

Regarding the proportion of time males spent in agonistic behaviors, the model produced significant results for the main factors, period and age, whereas the interaction term, period × age, was slightly nonsignificant (period: $F_{5,132} = 10.50$, $P < 0.0001$; age: $F_{1,29} = 10.88$, $P = 0.003$; age × period: $F_{5,132} = 2.12$, $P = 0.067$). Thus, the proportion of time allocated to agonistic behaviors generally declined from prerut to the rut. However, in contrast to the young males, whose prerut level remained on average around 4%, old males increased the time spent in agonistic behaviors during the prerut from about 5% to 12.5% (Figure 1). Overall, agonistic behaviors represented, on average, <2% of their daily time budgets during the first 6 weeks of the rut. Only during the last 2 weeks, older males showed a marked increase to about 10%.

Fights

Overall, 76 fights among at least 62 different male dyads were recorded during the 3 years of the study. Analyses showed that the number of dyads whose males engaged in fights differed between the prerut and the rut period. Accordingly, while accounting for the factors year and observation effort model comparisons revealed a significant effect of the interaction period × fight (df = 5, $\chi^2 = 15.1$, $P = 0.01$). Examination of the numbers of dyads in which fights could be observed revealed that during the prerut seasons, dyads with fights were more frequent than expected by chance (36 observed, 18.9 expected), whereas the opposite was the case for the rutting periods (32 observed, 49.1 expected). These patterns remained the same, also when analyzing the classes of young (≤8 years; prerut: 13 observed, 7.4 expected; rut: 13 observed, 18.6 expected) and old (≥9 years; prerut: 11 observed, 6.6 expected; rut: 15 observed, 19.4 expected) males separately (young males: df = 5, $\chi^2 = 13.5$, $P = 0.02$; old males: df = 5, $\chi^2 = 20.9$ $P < 0.001$).

Fights and takeovers

In none of the observed 176 takeovers (72, 58, and 46 in the 3 years [2005–2006 to 2007–2008], respectively) males were involved in fights (Binomial test for dyads: 2005–2006: N = 35, exceptions = 0, $P < 0.0001$; 2006–07: N = 54, exceptions = 0,

$P < 0.0001$, 2007–2008: N = 33, exceptions = 0, $P < 0.0001$), meaning that all observed takeovers happened without any foregoing fights among males in all 3 years.

DC of dyadic relationships

Estimated DC indices for the dominance relationships during the prerut periods in November–December of 2005, 2006, and 2007 were 1.0, 0.94, and 0.92, respectively (for details see Table 1). During the consecutive rutting periods the corresponding DC values of the dominance relationships ranged between 0.93 and 0.97. Regarding the takeover, inheritance, and tend–course situations, the estimated DC indices even took on values between 0.95 and 1.0 (Table 1).

Having a closer look at the few detected inconsistent dyads (i.e., dyads with changing winners) of the dominance situations during the prerut and rutting periods, it turned out that, in 16 of the 29 dyads, the concerned males had also been observed engaging in fights with each other. The number of fights within these dyads was by far higher than expected by chance (Binomial test: expected number of fights: 3.55, observed number of fights: 16, N = 29, $P < 0.0001$).

Regarding the outliers in the access-to-female situations, it can be noted that in the case of the only inconsistent takeover situation in 2007–2008, as well as in 2 of the 3 inconsistent tend–course situations in 2007–2008, male dyads were involved, which also showed inconsistencies in the dominance relationship during the rut.

Age differences

Further analyses of the dominance and fighting data showed that the age difference between interacting males had a clear negative effect on the proportion of inconsistent dyads (Spearman rank correlation, N = 12, $r_s = -0.94$, $P < 0.0001$) and on the proportion of observed fights per number of possible dyads (Spearman rank correlation, N = 14, $r_s = -0.90$, $P < 0.0001$). Thus, inconsistencies in dominance relationships became less frequent the bigger the age difference between the 2 dyad members. Analogously, the proportion of detected fights decreased with increasing age differences of interacting males (Figure 2).

Temporal stability of dominance relationships

Analyses of male dyads that were observed interacting during the prerut and the following rutting seasons showed that the dominance relationships mostly remained stable. Thus, in

Table 1
Summary of the number of observed interaction encounters during the prerut and rutting periods in 2005–2006, 2006–2007, and 2007–2008, respectively, with regard to dominance, takeover, inheritance, and tend-course situations

		Dominance			Takeover			Inheritance			Tend-course		
		2005–2006	2006–2007	2007–2008	2005–2006	2006–2007	2007–2008	2005–2006	2006–2007	2007–2008	2005–2006	2006–2007	2007–2008
Prerut	Observed dyads	39	109	83									
	Dyads with ≥2 encounters	26	43	37									
	Inconsistent relationships	0	5	5									
	DC index	1.00	0.94	0.92									
Rut	Observed dyads	100	122	229	35	53	33	16	12	17	92	177	185
	Dyads with ≥2 encounters	60	47	112	11	3	10	3	2	3	43	70	62
	Inconsistent relationships	6	3	10	0	0	1	0	0	0	0	0	2
	DC index	0.94	0.97	0.93	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	0.99

DC indices and the number of inconsistent relationships were calculated using Matman 1.1 (Noldus; De Vries et al. 1993; De Vries 1998).
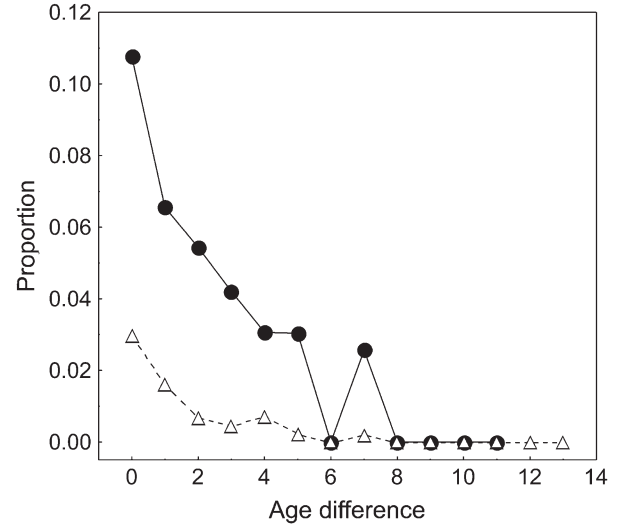
Figure 2
Proportion of inconsistent dyads per observed dyads (filled circles, solid line) and proportion of fights per possible dyads (open triangles, dashed line) in relation to age differences of interacting males during prerut and rutting periods in 2005–2006, 2006–2007, and 2007–2008.

2005–2006, for 11 of 12 (92%) dyads, the dominant animals in the prerut period were also the dominant animals in the rutting period; this was also the case for 16 of 18 (89%) dyads in 2006–2007, and 15 of 19 (79%) dyads in 2007–08 (Binomial test for all, $P < 0.02$). Age differences in the 7 dyads with changing dominant relationships were 0, 1, 1, 1, 2, 4, and 4 years. It should furthermore be noted that 1 specific individual (aged 10–12 years during the time of the study) was involved in 5 of a total of 7 dyads with changing dominance relationships.

Correspondence of dominance and access-to-females relationships

In 88.9–100% of the dyads, depending on the investigated category (i.e., takeover, inheritance, and tend–course situation) and the year of observation, the winner of interaction encounters coincided with the winner of access-to-female situations during the rut (Table 2). Hence, typically the dominant of 2 males gained (takeover situation) and held (tend–course situation) unrestricted access to a specific female, whereas the subordinate male had to leave or to wait in the vicinity of the consort pair. In all situations, where the dominant tending male left the female deliberately, a subordinate, and until then coursing, male obtained unrestricted access to the female (inheritance situation; Table 2).

In the 9 cases where the dominance relationships did not correspond with the outcome of the access-to-female situations, 5 different male dyads were involved overall (1 in 2005–2006, 1 in 2006–2007, and 3 in 2007–2008). In the 2 dyads, for which we have the necessary data (i.e., dominance relationships based on multiple interactions encounters), inconsistencies in the dominance relationships during the rut were detected.

DISCUSSION

In support of our hypothesis, the results showed that male Alpine ibex markedly reduced intramale competitions during the rut. They substantially cut down on the time they allocated

Table 2

Comparisons of the winners in male dyads determined by the dominance relationships with the winners determined by the different access-to-female situations for the different rutting periods 2005–2006, 2006–2007, and 2007–2008, respectively

	Takeover			Inheritance			Tend–course		
	2005–2006	2006–2007	2007–2008	2005–2006	2006–2007	2007–2008	2005–2006	2006–2007	2007–2008
Dyads of which the dominance relationship is known	19	25	27	13	7	10	48	67	97
Dyads where winner by dominance is winner by access-to-female relationship	18 (94.7%)	24 (96.0%)	24 (88.9%)	13 (100%)	7 (100%)	10 (100%)	47 (97.9%)	67 (100%)	94 (96.9%)
Binomial test P (2-tailed)	<0.0001	<0.0001	<0.0001	0.0002	0.016	0.002	<0.0001	<0.0001	<0.0001

Indicated are the number of dyads.

to agonistic behaviors and decreased the number of fights during the mating season compared with before the rut. This pattern was not only observed among young males but also among older males. Previous observations of the same population suggest that this pattern cannot be the result of a low level of intramale competition, because single receptive females were associated with, on average, 4 and up to a maximum of 11 males trying to gain mating access to receptive females (Willisch and Neuhaus 2009). This finding is particularly interesting as it contradicts the common assumption that the level of aggression in polygynous species should peak during the mating season when the value of the disputed resource is the highest (Parker 1974; Hsu et al. 2005).

Indeed, a comparison of the temporal occurrence and frequency of agonistic behaviors in male Alpine ibex with other polygynous ungulates shows that the detected pattern in Alpine ibex can be considered to be rather atypical. Hence, in 10 of 11 other reviewed ungulate species, for which quanti-

tative data was available, some or all agonistic behaviors culminated concomitantly with mating activities, suggesting that intramale interactions are usually more frequent when males compete for females in estrous (Table 3).

The question therefore arises, how male Alpine ibex can circumvent time- and energy-consuming interactions, which are ordinarily necessary to resolve these conflicts of interest? The results of our study indicate that a likely mechanism permitting this rather uncommon behavioral pattern is the establishment of stable and strictly binding dominance relationships among individual males, which makes fighting for access over disputed resources, such as mating partners, unnecessary. Accordingly, we could demonstrate that mainly prior to the rut and, under certain circumstances during the rut, consistent dominance relationships between individual pairs of male Alpine ibex were established that determined which 1 of the 2 males in a dyad would gain, inherit, or hold access to females. In addition, we also showed that physical aggression in the form of

Table 3

Number of populations in which agonistic behaviors culminate before or concomitantly with the peak of mating activity

	Before mating peak	During mating peak	References
Bovidae			
Bison bison		2 (AG, DP, and FT)	Komers et al. (1992, 1994a, 1994b), Wolff (1998)
Capra ibex	1 (AG, FT)		This study
Capra pyrenaica	1 (AG)		Alados (1986)
Rupicapra rupicapra		1 (AG)	Willisch (unpublished data)
Cervidae			
Alces alces		1 (FT)	Miquelle (1990)
Antilocapra americana		2 (AG)	Maher (1991, 1994)
Capreolus capreolus		1 (AG)	Melis et al. (2005)
Cervus elaphus		1 (DP, FT)	Clutton-Brock and Albon (1979), Clutton-Brock et al. (1979, 1982)
Cervus nippon		1 (AG)	Buschhaus et al. (1990), Miura (1984)
Dama dama	1 (DP)	3 (AG, DP, and FT)	Buschhaus et al. (1990), Clutton-Brock, Green et al. (1988), McElligott et al. (1998, 1999), Pelabon et al. (1999)
Odocoileus hemionus	2 (AG, rFT[a])	1 (AG, sFT[a])	Koutnik (1981), Kucera (1978)
Odocoileus viriginianus	2 (FT)	1 (AG)	Hirth (1977)

Behavioral categories: AG: agonistic behavior in general; DP: displacements; and FT: fights.

[a] Kucera (1978) distinguished between a "ritualized" (r) and a "serious" (s) form of fighting (antler locking, pushing, and twisting). He described the latter one to be more violent, but provided unfortunately no clear definition.

fights, although occurring during the mating season, was never used to gain or maintain access to specific receptive females. Males only fought to clarify their dominance relationships. This was further corroborated by the fact that fights were much more frequent than expected by chance among male dyads that had presented inconsistencies in their dominance relationships.

The observation that the proportion of inconsistencies and the observed number of fights were negatively correlated with the age differences among competing males further indicates that body size and, consequently, fighting ability of the contestants were playing a major role. Thus, in agreement with other studies (Clutton-Brock et al. 1979; McElligott et al. 1998; Pelletier and Festa-Bianchet 2006) also on Alpine ibex, the engagement in escalating interactions (i.e., fights) and potential changes in the dominance relationships were more likely to occur when animals were close in age and/or size. Nevertheless, it is important to stress that once the dominance relationships were established, subordinate male Alpine ibex, irrespective of their age and rank, did not challenge dominant males to force access to receptive females.

Overall the establishment of stable dominance relationships seems to be widespread among socially living animals, including males of some ungulates (e.g., fallow deer, *Dama dama*: McElligott et al. 1998; Jennings et al. 2006; bighorn sheep, *O. canadensis*: Pelletier and Festa-Bianchet 2006; and red deer, *Cervus elaphus*: Appleby 1982). Nevertheless, among these species, intense agonistic interactions for access to receptive females often appear to persist at high levels during the rut and are thus not reduced. For example, in red deer and fallow deer, fights between mature males are frequent during the rut and generally reported to increase in close relation with the number of observed matings (Clutton-Brock et al. 1979; McElligott et al. 1998) despite the existence of established dominance hierarchies among males in both species (Appleby 1982; McElligott et al. 1998). Furthermore, in feral goats (*Capra hircus*), bighorn sheep, and Soay sheep (*Ovis aries*) which have mating systems similar to the one found in Alpine ibex, subordinate males, which are typically excluded by dominant ones from access to single receptive females, are known to make frequent use of overt aggression (including horn clashes and flank butts) against the dominant, access-defending male in order to create transient mating opportunities (Hogg 1987; Preston et al. 2001; Saunders et al. 2005).

The ordinarily observed offensive use of aggression by males of polygynous ungulates, which ultimately reflects the high value of the female mating partners (Parker 1974; Hsu et al. 2005), contrasts sharply with the conservative behavior exhibited by male Alpine ibex during the rut. Hence, subordinate male Alpine ibex behaved, overall, very reluctantly toward their dominant competitors. Overt aggression was never used by subordinates as a means to achieve access to receptive females (as is often the case in polygynous species, see above) and they usually evaded dominant males when being approached by them (Willisch CS, personal observation). As a consequence, subordinate males either left receptive females tended by dominant males or they adopted the coursing tactic (Willisch and Neuhaus 2009). They never tried to create mating opportunities themselves by attacking the tending male. Only dominant, tending males displaced subordinate, coursing males by the use of offensive aggression when the latter were too close to the defended females. Lastly, subordinate male Alpine ibex were never observed to disturb mating attempts by dominant males, which is a behavior that has been observed in various other species, such as American bison (*Bison bison*, Lott 1981), reindeer (*Rangifer tarandus*, Hirotani 1994), or kafue lechwe (*Kobus leche*, Nefdt 1995; Nefdt and Thirgood 1997).

Considering the supposedly high value of the disputed resources, namely the receptive females, it may not be very evident, at first glance, as to why subordinate male Alpine ibex adhere so strictly to the established dominance relationships and why they do not try more actively to create mating opportunities by attacking and challenging dominant, tending males (Parker 1974; Hsu et al. 2005). Life-history theory, however, suggests that associated costs might be too high compared with the minor benefits, likely gained, in the form of few achieved paternities (Willisch CS, unpublished data). Accordingly, young male Alpine ibex might face a serious danger of compromising their potentially high future reproductive success (Pianka and Parker 1975) when incurring significant energy expenditures during the rut and taking into account increased risks of injury and mortality (Stevenson and Bancroft 1995; Stevenson et al. 2004). Because Alpine ibex males have to attain a relatively old age, of about 9 years, before becoming large (see Lüps et al. 2007) and competitive enough to tend receptive females, as suggested by Willisch and Neuhaus (2009), they have to be more cautious each year, in order to attain that critical age, than species who start to reproduce earlier in life, such as, red deer (5 years; Clutton-Brock, Albon, and Guinness 1988), fallow deer (4 years; McElligott and Hayden 2000), bighorn sheep (2–3 years; Hogg and Forbes 1997; Coltman et al. 2002) and Soay sheep (0–1 years; Coltman et al. 1999). This is because the overall chance of survival, over a certain number of years, declines exponentially with the number of years to survive. Overt and costly mating behavior may not only contribute to elevated mortality risks but may also contribute to depressed growth rates in young males. As body size is likely to be an important determinant of dominance in ungulates (Pelletier and Festa-Bianchet 2006), reduced growth may lead to below average adult body sizes, resulting ultimately in inferior reproductive potential and success (Stevenson et al. 2004). Given that animals are likely to vary their investments into current reproduction, with regard to their survival and growth perspectives, and hence, their potential future reproductive success, as suggested by life-history theory (Stearns 1992), a trade-off between the cost–benefit ratio of investments into overt aggression and the cost–benefit ratio of investments into survival and growth should be expected among male Alpine ibex (but see McElligott et al. 2002; Pelletier et al. 2006). Considering that the rut in male Alpine ibex takes place in very exposed and dangerous areas (i.e., vertical cliffs), and under extreme climatic conditions (with a lot of snow and freezing temperatures), our results indicate that the risks of depressed future reproductive success, through a likely increase in injury and mortality risks, as well as energy expenditures, apparently exceed the benefits of current reproductive success leading to the evolution of the detected reluctance in coursing behavior in male Alpine ibex. Hence, in Alpine ibex, the use of overt aggression against tending males might be much costlier with regard to the potential benefits than in other more overtly competing ungulates, such as for instance, bighorn sheep (Hogg and Forbes 1997) or feral goats (Saunders et al. 2005). This interpretation would, moreover, fit with the observation that the coursing tactic adopted mainly by young, subordinate male Alpine ibex involves only a relatively small proportion of high-cost behaviors and, in turn, a large proportion of low-cost behaviors when compared with males of other species (Willisch and Neuhaus 2009).

Whatever the ultimate reasons, the fact that male Alpine ibex reduce their agonistic interactions during the rut, including energy-intensive fights, is likely to have important implications for their energy budgets and their subsequent survival during winter. As shown in Table 3, in most polygynous ungulates,

agonistic behaviors typically peak at the time of year when females are receptive and when males have already invested much of their time and energy to courtship and mating behaviors. Together with severe reductions in restoring activities, such as feeding and/or lying (Miquelle 1990; Pelletier 2005; Willisch and Ingold 2007), the high energy expenditures due to agonistic interactions inevitably lead to negative energy budgets (Pelletier 2005; but see McElligott et al. 2003), which contribute to drastic losses in body weight and fat reserves of males (Bobek et al. 1990; Yoccoz et al. 2002; McElligott et al. 2003; Mysterud et al. 2004, 2005; Forsyth et al. 2005) and ultimately, to elevated mortality risks (Stevenson and Bancroft 1995; Stevenson et al. 2004). Because male Alpine ibex allocate very little time to agonistic behaviors during the rut, a significant component of their energetic expenditures will be substantially reduced in contrast to other species. This is likely to have positive effects on the body condition of males and their subsequent winter survival. The finding that reductions in agonistic interactions and fights were not only restricted to young males suggests that older, full-grown individuals might also profit from associated benefits. Overall, our study provides evidence that the excellent survival of adult male Alpine ibex, detected by Toïgo et al. (2007), might at least partially result from the specific social system in male Alpine ibex.

REFERENCES

Aeschbacher A. 1978. Das Brunftverhalten des Alpensteinbocks. Erlenbach-Zürich (Switzerland): Eugen Rentsch Verlag.

Alados CL. 1986. Aggressive behavior, sexual strategies and their relation to age in male Spanish ibex (*Capra pyrenaica*). Behav Proc. 12:145–158.

Altmann J. 1974. Observational study of behavior—sampling methods. Behaviour. 49:227–267.

Alvarez F. 1993. Risks of fighting in relation to age and territory holding in fallow deer. Can J Zool Rev Can Zool. 71:376–383.

Apollonio M, Festa-Bianchet M, Mari F, Riva M. 1990. Site-specific asymmetries in male copulatory success in a fallow deer lek. Anim Behav. 39:205–212.

Appleby MC. 1982. The consequences and causes of high social rank in red deer stags. Behaviour. 80:259–273.

Bartos L, Fricova B, Bartosova-Vichova J, Panama J, Sustr P, Smidova E. 2007. Estimation of the probability of fighting in fallow deer (*Dama dama*) during the rut. Aggress Behav. 33:7–13.

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

Buschhaus NL, Lagory KE, Taylor DH. 1990. Behavior in an introduced population of fallow deer during the rut. Am Midl Nat. 124:318–329.

Clutton-Brock TH, Albon SD. 1979. Roaring of red deer and the evolution of honest advertisement. Behaviour. 69:145–170.

Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE. 1979. Logical stag—adaptive aspects of fighting in red deer (*Cervus elaphus L*). Anim Behav. 27:211–225.

Clutton-Brock TH, Albon SD, Guinness FE. 1988. Reproductive success in male and female red deer. In: Clutton-Brock TH, editor. Reproductive success. Studies of individual variation in contrasting breeding systems. Chicago (IL): The University of Chicago Press. p. 325–343.

Clutton-Brock TH, Green D, Hiraiwa-Hasegawa M, Albon SD. 1988. Passing the buck: resource defence, lek breeding and mate choice in fallow deer. Behav Ecol Sociobiol. 23:281–296.

Clutton-Brock TH, Guinness FE, Albon SD. 1982. Red deer. Behavior and ecology of two sexes. Chicago (IL): The University of Chicago Press.

Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C. 2002. Age-dependent sexual selection in bighorn rams. Proc Roy Soc Lond Ser B Biol Sci. 269:165–172.

Coltman DW, Smith JA, Bancroft DR, Pilkington J, MacColl ADC, Clutton-Brock TH, Pemberton JM. 1999. Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. Am Nat. 154:730–746.

Conradt L, Roper TJ. 2000. Activity synchrony and social cohesion: a fission-fusion model. Proc Roy Soc Lond Ser B Biol Sci. 267: 2213–2218.

Crawley MJ. 2007. The R book. Chichester (United Kingdom): John Wiley & Sons Ltd.

De Vries H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim Behav. 55: 827–843.

De Vries H, Netto WJ, Hanegraaf PLH. 1993. Matman—a program for the analysis of sociometric matrices and behavioral transition matrices. Behaviour. 125:157–175.

Drews C. 1993. The concept and definition of dominance in animal behavior. Behaviour. 125:283–313.

Forsyth DM, Duncan RP, Tustin KG, Gaillard JM. 2005. A substantial energetic cost to male reproduction in a sexually dimorphic ungulate. Ecology. 86:2154–2163.

Fryxell JM. 1987. Lek breeding and territorial aggression in white-eared kob. Ethology. 75:211–220.

Hirotani A. 1994. Dominance rank, copulatory behavior and estimated reproductive success in male reindeer. Anim Behav. 48: 929–936.

Hirth DH. 1977. Social behavior of white-tailed deer in relation to habitat. Wildl Monogr. 53:3–55.

Hoem SA, Melis C, Linnell JDC, Andersen R. 2007. Fighting behaviour in territorial male roe deer *Capreolus capreolus*: the effects of antler size and residence. Eur J Wildl Res. 53:1–8.

Hogg JT. 1984. Mating in bighorn sheep—multiple creative male strategies. Science. 225:526–529.

Hogg JT. 1987. Intrasexual competition and mate choice in Rocky mountain bighorn sheep. Ethology. 75:119–144.

Hogg JT, Forbes SH. 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk "'unconventional" tactic. Behav Ecol Sociobiol. 41:33–48.

Hsu Y, Earley RL, Wolf LL. 2005. Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. Biol Rev. 80:1–42.

Jennings DJ, Gammell MP, Carlin CM, Hayden TJ. 2003. Is the parallel walk between competing male fallow deer, *Dama dama*, a lateral display of individual quality? Anim Behav. 65:1005–1012.

Jennings DJ, Gammell MP, Carlin CM, Hayden TJ. 2006. Is difference in body weight, antler length, age or dominance rank related to the number of fights between fallow deer (*Dama dama*)? Ethology. 112:258–269.

Komers PE, Messier F, Gates CC. 1992. Search or relax—the case of bachelor wood bison. Behav Ecol Sociobiol. 31:195–203.

Komers PE, Messier F, Gates CC. 1994a. Plasticity of reproductive behavior in wood bison bulls—on risks and opportunities. Ethol Ecol Evol. 6:481–495.

Komers PE, Messier F, Gates CC. 1994b. Plasticity of reproductive behavior in wood bison bulls—when subadults are given a chance. Ethol Ecol Evol. 6:313–330.

Koutnik DL. 1981. Sex related differences in the seasonality of agonistic behavior in mule deer. J Mammal. 62:1–11.

Kucera TE. 1978. Social behavior and breeding system of desert mule deer. J Mammal. 59:463–476.

Lott DF. 1981. Sexual behavior and intersexual strategies in American bison. Zeitschr Tierpsychol J Comp Ethol. 56:97–114.

Lüps P, Blöchlinger B, Schmid P, Zuber M. 2007. Ontogenese und Variabilität verschiedener Körpermerkmale des Steinwildes *Capra i. ibex* im Berner Oberland (Schweizer Alpen). Beiträge Jagd Wildforsch. 32:495–510.

Maher CR. 1991. Activity budgets and mating system of male pronghorn antelope at Sheldon National Wildlife Refuge, Nevada. J Mammal. 72:739–744.

Maher CR. 1994. Pronghorn male spatial organization—population differences in degree of nonterritoriality. Can J Zool Rev Can Zool. 72:455–464.

Mainguy J, Cote SD, Cardinal E, Houle M. 2008. Mating tactics and mate choice in relation to age and social rank in male mountain goats. J Mammal. 89:626–635.

McElligott AG, Altwegg R, Hayden TJ. 2002. Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*). Proc Roy Soc Lond Ser B Biol Sci. 269:1129–1137.

McElligott AG, Hayden TJ. 2000. Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*). Behav Ecol Sociobiol. 48:203–210.

McElligott AG, Mattiangeli V, Mattiello S, Verga M, Reynolds CA, Hayden TJ. 1998. Fighting tactics of fallow bucks (*Dama dama*, Cervidae): reducing the risks of serious conflict. Ethology. 104:789–803.

McElligott AG, Naulty F, Clarke WV, Hayden TJ. 2003. The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? Evol Ecol Res. 5:1239–1250.

McElligott AG, O'Neill KP, Hayden TJ. 1999. Cumulative long-term investment in vocalization and mating success of fallow bucks, *Dama dama*. Anim Behav. 57:1159–1167.

Melis C, Hoem SA, Linnell JDC, Andersen R. 2005. Age-specific reproductive behaviours in male roe deer *Capreolus capreolus*. Acta Theriol. 50:445–452.

Miquelle DG. 1990. Why dont bull moose eat during the rut. Behav Ecol Sociobiol. 27:145–151.

Miura S. 1984. Social behavior and territoriality in male sika deer (*Cervus nippon* Temminck 1838) during the rut. Zeitschr Tierpsychol J Comp Ethol. 64:33–73.

Moore NP, Kelly PF, Cahill JP, Hayden TJ. 1995. Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. Behav Ecol Sociobiol. 36:91–100.

Mysterud A, Langvatn R, Stenseth NC. 2004. Patterns of reproductive effort in male ungulates. J Zool. 264:209–215.

Mysterud A, Solberg EJ, Yoccoz NG. 2005. Ageing and reproductive effort in male moose under variable levels of intrasexual competition. J Anim Ecol. 74:742–754.

Nefdt RJC. 1995. Disruptions o matings, harassment and lek-breeding in kafue lechwe antelope. Anim Behav. 49:419–429.

Nefdt RJC, Thirgood SJ. 1997. Lekking, resource defense, and harassment in two subspecies of lechwe antelope. Behav Ecol. 8:1–9.

Olsson M. 1993. Contest success and mate guarding in male sand lizards, *Lacerta agilis*. Anim Behav. 46:408–409.

Parker GA. 1974. Assessment strategy and evolution of fighting behavior. J Theor Biol. 47:223–243.

Parrini F, Grignolio S, Luccarini S, Bassano B, Apollonio M. 2003. Spatial behaviour of adult male Alpine ibex *Capra ibex ibex* in the Gran Paradiso National Park, Italy. Acta Theriol. 48:411–423.

Pelabon C, Komers PE, Birgersson B, Ekvall K. 1999. Social interactions of yearling male fallow deer during rut. Ethology. 105:247–258.

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

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

Pelletier F, Hogg JT, Festa-Bianchet M. 2006. Male mating effort in a polygynous ungulate. Behav Ecol Sociobiol. 60:645–654.

Pianka ER, Parker WS. 1975. Age-specific reproductive tactics. Am Nat. 109:453–464.

Pinheiro JC, Bates DM. 2000. Mixed-effects models in S and S-Plus. New York: Springer Verlag.

Preston BT, Stevenson IR, Pemberton JM, Wilson K. 2001. Dominant rams lose out by sperm depletion—a waning success in siring counters a ram's high score in competition for ewes. Nature. 409:681–682.

Ratti P, Habermehl KH. 1977. Investigations into age determination of mountain Ibex (*Capra–Ibex–Ibex*) in Kanton Graubunden. Zeitschr Jagdwissensch. 23:188–213.

Saunders FC, McElligott AG, Safi K, Hayden TJ. 2005. Mating tactics of male feral goats (*Capra hircus*): risks and benefits. Acta Ethol. 8:103–110.

Sheskin DJ. 2004. Handbook of parametric and nonparametric statistical procedures. 3rd ed. Boca Raton (FL): Chapman & Hall/CRC.

Stearns SC. 1992. The evolution of life histories. New York: Oxford University Press.

Stevenson IR, Bancroft DR. 1995. Fluctuating trade-offs favour precocial maturity in male Soay sheep. Proc Roy Soc Lond Ser B Biol Sci. 262:267–275.

Stevenson IR, Marrow P, Preston BT, Pemberton JM, Wilson K. 2004. Adaptive reproductive strategies. In: Clutton-Brock TH, Pemberton J, editors. Soay sheep. Dynamics and selection in a island population. Cambridge (MA): Cambridge University Press.

Taillon J, Coté SD. 2006. The role of previous social encounters and body mass in determining social rank: an experiment with white-tailed deer. Anim Behav. 72:1103–1110.

Toigo C, Gaillard JM. 2003. Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? Oikos. 101:376–384.

Toïgo C, Gaillard JM, Festa-Bianchet M, Largo E, Michallet J, Maillard D. 2007. Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. J Anim Ecol. 76:679–686.

Villaret JC, Bon R. 1998. Sociality and relationships in Alpine ibex (*Capra ibex*). Rev Ecol Terre Vie. 53:153–170.

Wells MS. 1988. Effects of body size and resource value on fighting behavior in a jumping spider. Anim Behav. 36:321–326.

Willisch CS. 2009. The ecology of reproduction in long-lived male Alpine ibex (*Capra ibex*): the role of age, dominance, and alternative mating tactics. PhD thesis. Neuchâtel (Switzerland): université de Neuchâtel. p. 110.

Willisch CS, Ingold P. 2007. Feeding or resting? The strategy of rutting male Alpine chamois. Ethology. 113:97–104.

Willisch CS, Neuhaus P. 2009. Alternative mating tactics and their impact on survival in adult male Alpine ibex (*Capra ibex ibex*). J Mammal. 90:1421–1430.

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

Yoccoz NG, Mysterud A, Langvatn R, Stenseth NC. 2002. Age- and density-dependent reproductive effort in male red deer. Proc Roy SocLond Ser B Biol Sci. 269:1523–1528.

Zar JH. 1999. Biostatistical analysis. 4th ed. London: Prentice-Hall.