The ecology of reproduction in long-lived male Alpine ibex (*Capra ibex*): The role of age, dominance and alternative mating tactics

---

Christian S. Willisch

Thesis presented the 25th May 2009 in presence of

Peter Neuhaus, University of Neuchâtel	Supervisor
Redouan Bshary, University of Neuchâtel	Examiner
Michael Taborsky, University of Berne	Examiner
Alan G. McElligott, Queen Mary University of London	Examiner

Université de Neuchâtel unine
Faculty of science
Department of Behavioural Ecology

Université de Neuchâtel unine

FACULTE DES SCIENCES
Secrétariat-Décanat de la faculté
- Rue Emile-Argand 11
- CP 158
- CH-2009 Neuchâtel

IMPRIMATUR POUR LA THESE

The ecology of reproduction in long-lived male Alpine ibex (*Capra ibex*): The role of age, dominance and alternative mating tactics

Christian WILLISCH

UNIVERSITE DE NEUCHATEL

FACULTE DES SCIENCES

La Faculté des sciences de l'Université de Neuchâtel,
sur le rapport des membres du jury

MM. R. Bshary (directeur de thèse), P. Neuhaus,
M. Taborsky (Berne) et A. McElligott (Londres)

autorise l'impression de la présente thèse.

Neuchâtel, le 9 juillet 2009

Le doyen :
F. Kessler

UNIVERSITE DE NEUCHATEL
FACULTE DES SCIENCES
Secrétariat - décanat de la faculté
Rue Emile-Argand 11 - CP 158
CH-2009 Neuchâtel

Felix Kessler

Contents

ABSTRACT

Recent studies on survival and growth in male Alpine ibex indicated that they might pursue a rather conservative reproductive strategy at young age. To investigate this, and the role of age, social dominance and the adoption of alternative mating tactics for the reproduction and survival of male Alpine ibex, I conducted behavioral observations during three consecutive rutting seasons in a population in the Swiss Alps, and inferred paternity in two offspring cohorts using molecular methods.

Since basic information on reproductive behaviour in male Alpine ibex was lacking, I provided in **chapter 1**, first a detailed description of the mating system and the two alternative mating tactics in this species. I then investigated to which extent the adoption of these observed mating tactics in male Alpine ibex can contribute to the exceptional survival described in this species. Some males adopted a tactic termed 'tending' to monopolize individual, receptive females by following and defending them persistently against their competitors that tried to sneak copulations via the so called 'coursing' tactic. The adoption of the two tactics was strongly age-dependent with older males engaging primarily in the tending tactic while younger males typically used the coursing tactic. With regard to the observed number of copulations, tending appeared to be the more successful tactic, although some copulations were also the result of coursing. However, males adopting the coursing tactic spent more time in low-cost and less time in high-cost behaviors than males adopting the tending tactic. Time budget comparisons with another ungulate species suggested that while tending is a relatively costly tactic, coursing is a low-cost tactic that might indeed contribute to the exceptional adult survival in male Alpine ibex.

Because of the supposed small energetic costs male Alpine ibex appeared to incur during the rut and the fact that they are aggregating in social groups, I tested in **chapter 2**, whether energy-intensive agonistic interactions among competing males might be reduced during the rut as a result of a pre-established and binding dominance hierarchies among them. In accordance with our hypothesis, male Alpine ibex decreased the time spent in agonistic interactions and the number of horn fights during the rut compared to the pre-rut. As expected, changes between access-holding males occurred always without foregoing horn fights and were entirely based on pre-established, stable dominance relationships. Subordinate males either left the consort pair or they adopted the coursing tactic in order to achieve temporary access to estrus females. They behaved extremely reluctant towards dominants, as they never used overt aggression to challenge them or to create actively transient mating opportunities. Overall, male Alpine ibex appeared to be able to cut down on energy-expenditures associated with agonistic interactions by the adherence to pre-established and stable dominance relationships among them, what in turn was likely to contribute to their superior survival.

In **chapter 3**, we analyzed within a Bayesian framework the effects of age, dominance and mating tactics on the likelihood of paternity in male Alpine ibex. Based on life-history considerations, reproductive success in male Alpine ibex was expected to be comparatively heavily skewed towards older, dominant males making primarily use of a tactic to monopolize access to receptive females, while younger, subordinate males trying to steal copulations from access-defending males via a ‘sneaking’ tactic were predicted to sire only sporadically offspring. In accordance with our hypothesis, reproductive success was heavily skewed towards older, dominant males that typically monopolized access to receptive females by the adoption of the ‘tending’ tactic, while success among young, subordinate males via the sneaking tactic ‘coursing’ was overall low and rare. Compared with other ungulates with higher mortality rates, reproduction among young male Alpine ibex was overall lower and more sporadic. Finally, a relatively high reproductive skew emerged, denoting a big potential for selection in male Alpine ibex. The findings support the theory that survival perspectives of males modulate the investments into reproduction via alternative mating tactics early in life.

This thesis provides for the first time quantitative data on reproductive behaviour of male Alpine ibex during the rut. It denotes the importance of age, social status and the adoption of alternative mating tactics for reproduction in male Alpine ibex. Furthermore, the results indicate that the life-history strategy of male Alpine ibex is likely to target for long life, slow and prolonged growth and late reproduction.

GENERAL INTRODUCTION

The various forms of life-histories found in animals can be considered to reflect the specific strategies individuals adopt to allocate the limited energy resources into current versus future reproduction (Kozlowski 1992). Because reproduction is costly (e.g, Stevenson & Bancroft 1995) and typically results in depressed future reproductive success (Bell 1980) the residual reproductive value of animals will decline once they have started to breed (Clutton-Brock 1984; Pianka & Parker 1975). Therefore, animals have to decide carefully when and where to invest the energy disposable to them in order to maximize their lifetime reproductive success. Because reproductive success is often found to be age and size-related, survival and growth are likely to be important components of individual life-time reproductive success in many iteroparous species (Stearns 1992). This suggests that the potential to reproduce is likely to vary among species exhibiting differing survival and growth rates. It is expected, that in species exhibiting high mortality rates, animals should start to reproduce early in life while in species with low mortality individuals are assumed to first invest into growth before starting to reproduce (Stearns 1992). In accordance with these expectations, meta-analyses of life history traits in a variety of animal species revealed, while accounting for differences in body size and phylogeny, that growth and survival indeed both co-varied with reproduction, (Dobson & Oli 2007; Promislow & Harvey 1990). Thus, short life was found to be associated with fast growth, early maturity and start of reproduction, as well as high rates of reproduction, whereas long life related to slow growth, delayed age of maturity and start of reproduction, and low rates of reproduction, (e.g., Dobson & Oli 2007; Harvey & Zammuto 1985; Promislow & Harvey 1990). The observed pattern of these interrelated life-history traits is in literature also referred to as the ‘slow-fast continuum’ denoting that animals vary with respect to these traits along a continuum between slow and fast life trajectories. To understand the evolution and the ecology of different life-history strategies in animals it is therefore indispensable to have a thorough knowledge of their age-dependent survival, growth and reproduction patterns (Stearns 1992).

Important components characterizing the pattern of reproduction are the costs and benefits of reproduction, as well as their timing with regard to the age of animals (Stearns 1992). These aspects become particularly interesting in polygynous species, such as ungulates, in which the potential of males to monopolize access to receptive females is culminating late in life when adult body size is reached (Clutton-Brock et al. 1979; Pelletier & Festa-Bianchet 2006). In these species, one would typically assume that animals should wait with reproduction until they are full-grown in order not to jeopardize their future reproductive success. However, genetic studies have revealed that in many ungulates reproductive success of males can be relatively high already early in life (e.g., Coltman et al. 2002; Roed et al. 2005; Sorin 2004). Compared to older males, whose reproductive success depends mainly on their ability to monopolize receptive females, success in young males is likely to be the result of alternative mating tactics involving sneaky behavioural elements to ‘steal’ copulations from access-defending males (Hogg & Forbes 1997; Isvaran 2005; Taborsky 1997; Wolff 2008). Contrary to common expectations that these behavioural tactics are generally relatively low-cost (Taborsky et al. 2008), evidence accumulated in males of polygynous ungulates that they can be energetically costly (Pelletier 2005) and bear increased risks of injury or death (Preston et al. 2001; Saunders et al. 2005).

The ecology of reproduction in long-lived male Alpine ibex (*Capra ibex*): The role of age, dominance and alternative mating tactics.

In this thesis I investigated the ecology of reproduction in male Alpine ibex, a mountain ungulate which recently was reported to exhibit an exceptionally high adult survival (Toïgo et al. 2007) in combination with a relatively slow and prolonged growth in body size (Lüps et al. 2007). Particularly, I was interested in how age, social status and the adoption of alternative mating tactics during the rut affected reproductive behaviour in males.

When I started with this thesis, only little information on reproductive behaviour of male Alpine ibex existed. To my knowledge, the only reliable work on this topic was published by Aeschbacher (1978). He provided detailed descriptions of certain behaviours in male and female Alpine ibex during the rut. While parts of his observations were conducted in a small zoo population, some were performed in a population of free-living Alpine ibex in the Swiss Alps. However, many of his findings and conclusions were based on rather anecdotal observations lacking confirmation by quantitative analyses of corresponding data. Unfortunately, he also omitted the classification of the male mating behaviours with regard to discontinuous forms of male mating phenotypes (Oliveira et al. 2008), although he perceived and described apparently some divergence in the mating behaviour among male Alpine ibex. This omission may have led to a somewhat blurred perception of male mating behaviour in Alpine ibex in the recent past, as it was often assumed that only the oldest males would engage in reproductive activities while younger individuals refrain completely from taking part in the rutting activities and not make use of alternative mating tactics (e.g., Toïgo et al. 2007). Despite the general lack of scientific studies on male reproductive behaviour, Alpine ibex were subject of a variety of investigations covering different aspects of their biology during the past decades. The most relevant ones for this thesis were the recently published works on their ontogeny and survival by Lüps et al. (2007) and by Toïgo et al. (2007), respectively. Both studies contain significant information on two major components characterizing the life trajectories of animals along the slow-fast continuum introduced above. Hence, Lüps et al. (2007) demonstrated by the use of various body measurements (such as weight, chest girth, withers height or body length) of animals that were shot between 1980 and 2005 in various populations in the Swiss Alps that male Alpine ibex do normally not reach asymptotic body size until the age of 8 years; hence relatively late in life compared to other male ungulates (e.g., red deer, *Cervus elaphus*: 6 years, Clutton-Brock et al. 1982; bighorn sheep, *Ovis canadenis*: 6 years, Pelletier & Festa-Bianchet 2006; Alpine chamois: *Rupicpara rupicapra*: 4 years, Bassano et al. 2003). The same pattern was also found using body weight data on hunted Alpine ibex between 1991 and 2006 in our study area (Gosselin 2008). Toïgo et al. (2007), on the other hand, showed that annual survival rates in adult males based on marked individuals in an unhunted population in the French Alps were extraordinarily high, exceeding survival of other male ungulates by 5-20%. Thus, survival rates of males aged 2-8 were reported to exceed on average 98% irrespective of the ecological conditions, whereas survival in males of 8-13 years of age ranged around 96% under good conditions, and around 85% when conditions were bad.

Considering the rather slow and prolonged growth in combination with the remarkable survival to a relatively high age, it turns out that male Alpine ibex differ in two important aspects of their life from many other polygynous ungulates for which comparable data can be found. This led Toïgo et al. (2007) to speculate that male Alpine ibex might ultimately also differ from other polygynous ungulates with regard to reproduction. Particularly, they expected male Alpine ibex to adopt a very conservative reproductive strategy allowing them to exhibit the high survival detected.

As basic information on the occurrence of alternative mating tactics in male Alpine ibex were missing, I provided in **chapter 1**, first a detailed description of the observed mating tactics in the study area, as well as information on the temporal and spatial distribution of receptive females, which were assumed to set the ecological outlines under which alternative mating tactics are likely to evolve (Shuster & Wade 2003). I then investigated to which extent the adoption of the observed mating tactics in male Alpine ibex contributed to their exceptional survival (Toïgo et al. 2007). Because of the supposed small energetic costs male Alpine ibex appeared to incur during the rut and the fact that they live in social groups year-round (Villaret & Bon 1998) I tested in **chapter 2**, whether energy-intensive agonistic interactions among competing males might be reduced during the rut by the adherence to pre-established dominance hierarchies among them. In **chapter 3**, I analyzed within a Bayesian framework the effects of age, dominance and mating tactics on the likelihood of paternity in male Alpine ibex. Based on life-history considerations, reproductive success in male Alpine ibex was expected to be comparatively heavily skewed towards older, dominant males making primarily use of a tactic to monopolize access to receptive females, while younger, subordinate males trying to steal copulations from access-defending males via a ‘sneaking’ tactic were predicted to sire only sporadically offspring.

The aim of this thesis was not only to present new and intriguing insights into the reproductive behaviour and ecology of an extremely long-lived, slowly and long growing mountain ungulate, but also to provide essential data to work out and improve management guidelines for this species. I am convinced that the incorporation of specific life-history data will be indispensable for a sustainable management of Alpine ibex in order to minimize the latent risks of negative consequences for their long evolved life-history traits (see e.g., (Coltman et al. 2003).

Study animals

Alpine ibex were extirpated by the 19th century due to over-hunting and poaching in all parts of the Alpine arc with exception of a small population that sustained in the region of the ‘*Gran Paradiso*’ mountain in the Italian Alps (Meile et al. 2003). First reintroduction programs of Alpine ibex started at the beginning of the 20th century in Switzerland. Since then Alpine ibex have successfully been reintroduced in most of parts of the Alps. In Switzerland, hunting of Alpine ibex under strict regulations has taken place since 1977 (Biebach 2009).

Alpine ibex are sexually dimorphic, with adult males being more than twice as heavy (95 kg versus 45 kg; Loison et al. 1999; Fig. 1) and possessing much larger horns than adult females (>90 cm versus >30 cm; Lüps et al. 2007). Because of the prolonged growth mentioned above, males of differing ages are showing pronounced size differences (Fig. 2) leading to supposedly marked age-dependent differences in individual fighting ability and dominance rank (Decristophoris et al. 2007).

The study was carried out between 2005 and 2008 in the Alpine ibex population ‘Cape au Moine’ (46° 22’ N; 07°09’ E, 1700-2550 m) north of the village Les Diablerets (VD) in the Swiss Alps (Fig. 3). The study area consisted mainly of a west-east directed, steep mountain ridge which was characterized by extensive open alpine pastures at higher altitudes and by patches of dense spruce forests (*Picea abies*) at lower altitudes (< 1800 m). The whole area was interspersed with rocky cliffs of varying size. In winter, the north side remained always covered by snow whereas on the south side usually substantial parts of the mountain ridge were free of snow due to solar radiation and avalanches.

Fig. 1. Alpine ibex during the rut. 13 year old male courting an adult female (foreground), while the kid and a 3 year old marked male (background) are waiting in their vicinity. Note the size differences between the old, full-grown male and the other animals.

Fig. 2. Size differences in male Alpine ibex of differing age classes. The ages of the individuals (from left to right) are 10, 6 and 3 years.

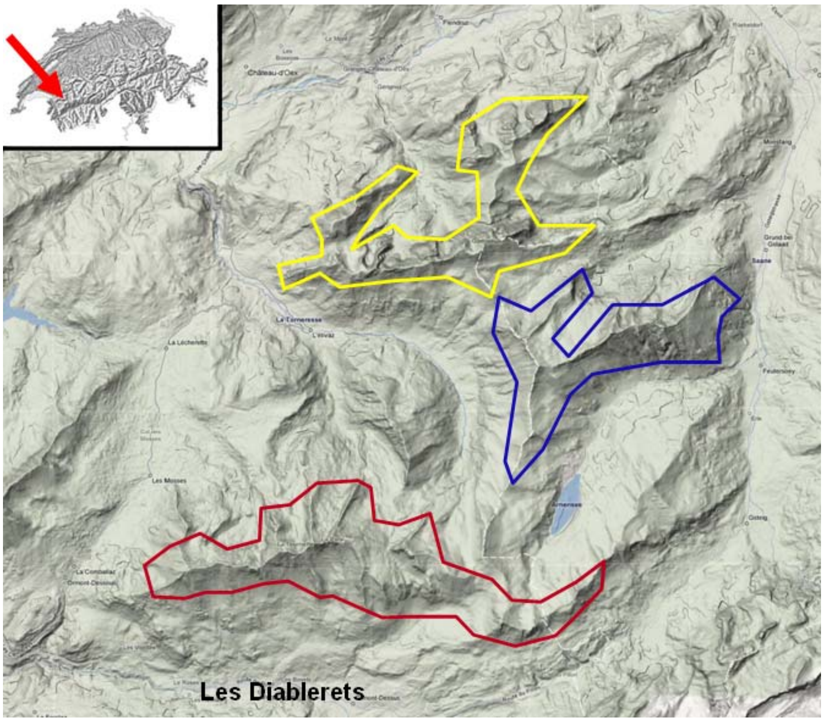

Fig. 3. Location of the Alpine ibex population ‘Cape au Moine’ (red) north of the village Les Diablerets (Canton Vaud), Switzerland. Male Alpine ibex are known to roam between this population and two adjacent populations further north (blue: ‘Wittenberg’ population; yellow: ‘Gummfluh / La Pierreuse’ population).

The population ‘Cape au Moine’ was founded by immigrating males from the two neighbouring populations ‘Wittenberg’ and ‘Gummfluh / La Pierreuse’ (Fig. 3; Baumann 2009). Estimated meta-population size was > 500 animals (data provided by the Federal Office of the Environment, Switzerland), while census during the study revealed that population size at Cape au Moine varied at less than 270 individuals. Females with young lived year-round in groups of up to 50 animals that were permanently resident in the study area. Males, on the other hand, formed loose groups of variable composition (see also Villaret & Bon 1998). Some males were evidenced to roam between Cape au Moine and the two adjacent populations. This roaming behaviour, which is also known from other ibex populations (Abderhalden 2005), seemed to be particularly apparent during the pre-rut period in November-December (see also Parrini et al. 2003). In late autumn and winter, the animals primarily inhabited the steep, south-facing mountain slopes and cliffs that were relatively free of snow, as has been reported for other populations of Alpine ibex (Grignolio et al. 2003). Potential natural predators of Alpine ibex present in the study area were: Eurasian lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), golden eagle (*Aquila chrysaetos*), and wolf (*Canis lupus*; since 2007; J.-C. Roch, pers. comm.).

Alpine ibex at Cape au Moine have been subject of strictly regulated hunting since 1991. Based on spring censuses, each autumn a limited number of animals were killed either by hunters or the local game wardens (Gosselin 2008).

References

Abderhalden, W. 2005: Raumnutzung und sexuelle Segregation beim Alpensteinbock *Capra ibex ibex*. Nationalpark-Forschung Schweiz **92**.

Aeschbacher, A. 1978: Das Brunftverhalten des Alpensteinbocks. Eugen Rentsch Verlag, Erlenbach-Zürich.

Bassano, B., Perrone, A. & Von Hardenberg, A. 2003: Body weight and horn development in Alpine chamois, *Rupicapra rupicapra* (Bovidae, Caprinae). Mammalia **67**, 65-73.

Baumann, P. W. 2009: Der Alpensteinbock. Ein Leben über dem Abrgund. hep verlag ag, Bern.

Bell, G. 1980: The costs of reproduction and their consequences. American Naturalist **116**, 45-76.

Biebach, I. 2009: Genetic structure, genetic diversity and inbreeding in reintroduced Alpine ibex (*Capra ibex ibex*) populations. Dissertation, University of Zürich, Zürich.

Clutton-Brock, T. H. 1984: Reproductive effort and terminal investment in iteroparous animals. American Naturalist **123**, 212-229.

Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979: Logical stag - adaptive aspects of fighting in red deer (*Cervus elaphus* L). Animal Behaviour **27**, 211-225.

Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982: Red deer. Behavior and ecology of two sexes. The University of Chicago Press, Chicago.

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

Coltman, D. W., O'Donoghue, P., Jorgenson, J. T., Hogg, J. T., Strobeck, C. & Festa-Bianchet, M. 2003: Undesirable evolutionary consequences of trophy hunting. Nature **426**, 655-658.

Decristophoris, P. M. A., von Hardenberg, A. & McElligott, A. G. 2007: Testosterone is positively related to the output of nematode eggs in male Alpine ibex (*Capra ibex*) faeces. Evolutionary Ecology Research **9**, 1277-1292.

Dobson, F. S. & Oli, M. K. 2007: Fast and slow life histories of mammals. Ecoscience **14**, 292-299.

Gosselin, F. 2008: Les effets de la densité de la population et des conditions climatiques de l'année de naissance sur la masse chez le bouquetin des alpes (*Capra ibex ibex*). Master thesis, Université de Neuchâtel, Neuchâtel.

Grignolio, S., Parrini, F., Bassano, B., Luccarini, S. & Apollonio, M. 2003: Habitat selection in adult males of Alpine ibex, *Capra ibex ibex*. Folia Zoologica **52**, 113-120.

Harvey, P. H. & Zammuto, R. M. 1985: Patterns of mortality and age at 1st reproduction in natural populations of mammals. Nature **315**, 319-320.

Hogg, J. T. & Forbes, S. H. 1997: Mating in bighorn sheep: Frequent male reproduction via a high-risk "unconventional" tactic. Behavioral Ecology and Sociobiology **41**, 33-48.

Isvaran, K. 2005: Variation in male mating behaviour within ungulate populations: patterns and processes. Current Science **89**, 1192-1199.

Kozlowski, J. 1992: Optimal allocation of resources to growth and reproduction - implications for age and size at maturity. Trends in Ecology & Evolution **7**, 15-19.

Loison, A., Gaillard, J. M., Pelabon, C. & Yoccoz, N. G. 1999: What factors shape sexual size dimorphism in ungulates? Evolutionary Ecology Research **1**, 611-633.

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 zur Jagd- und Wildforschung **32**, 495-510.

Meile, P., Giacometti, M. & Ratti, P. 2003: Der Steinbock. Biologie und Jagd. Salm Verlag., Bern.

Oliveira, R. F., Taborsky, M. & Brockmann, H. J. 2008: Alternative reproductive tactics. An integrative approach. Cambridge University Press, Cambridge.

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 Theriologica **48**, 411-423.

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

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

Pianka, E. R. & Parker, W. S. 1975: Age-specific reproductive tactics. American Naturalist **109**, 453-464.

Preston, B. T., Stevenson, I. R., Pemberton, J. M. & 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.

Promislow, D. E. L. & Harvey, P. H. 1990: Living fast and dying young - a comparative-analysis of life-history variation among mammals. Journal of Zoology **220**, 417-437.

Roed, K. H., Holand, O., Gjostein, H. & Hansen, H. 2005: Variation in male reproductive success in a wild population of reindeer. Journal of Wildlife Management **69**, 1163-1170.

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

Shuster, S. M. & Wade, M. J. 2003: Mating systems and strategies. Princeton University Press, Princeton.

Sorin, A. B. 2004: Paternity assignment for white-tailed deer (*Odocoileus virginianus*): Mating across age classes and multiple paternity. Journal of Mammalogy **85**, 356-362.

Stearns, S. C. 1992: The evolution of life histories. Oxford University Press, New York.

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

Taborsky, M. 1997: Bourgeois and parasitic tactics: do we need collective, functional terms for alternative reproductive behaviours? Behavioral Ecology and Sociobiology **41**, 361-362.

Taborsky, M., Oliveira, R. F. & Brockmann, H. J. 2008: The evolution of alternative reproudctive tactics: concepts and questions. In: Alternative reproductive tactics. An integrative approach. (Oliveira, R. F., Taborsky, M. & Brockmann, H. J. eds). Cambrigde University Press, Cambridge.

Toïgo, C., Gaillard, J. M., 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. Journal of Animal Ecology **76**, 679-686.

Villaret, J. C. & Bon, R. 1998: Sociality and relationships in Alpine ibex (*Capra ibex*). Revue D Ecologie-La Terre Et La Vie **53**, 153-170.

Wolff, J. O. 2008: Alternative reproductive tactics in nonprimate male mammals. In: Alternative reproductive tactics. An integrative approach. (Oliveira, R. F., Taborsky, M. & Brockmann, H. J. eds). Cambridge University Press, Cambridge. pp. 356-372.

CHAPTER 1

ALTERNATIVE MATING TACTICS AND THEIR IMPACT ON SURVIVAL IN ADULT MALE ALPINE IBEX (*CAPRA IBEX IBEX*)

Christian S. Willisch & Peter Neuhaus

Accepted for publication in *Journal of Mammalogy.*

Corresponding author:
Christian S. Willisch
Department of Eco-Ethology, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2009 Neuchâtel, Switzerland
Email: willichristian@yahoo.com

Running title:
Mating tactics & survival in Alpine ibex

Print title:
ALTERNATIVE MATING TACTICS AND THEIR IMPACT ON SURVIVAL IN ADULT MALE ALPINE IBEX (*CAPRA IBEX IBEX*)

Authors:
Christian S. Willisch[1)] and Peter Neuhaus[1,2)]

Addresses:
1) Department of Eco-Ethology, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2009 Neuchâtel, Switzerland

2) Department of Biological Sciences, University of Calgary, 2500 University Dr. NW, Calgary AB, T2N 1N4, Canada

ABSTRACT

Adult male Alpine ibex (*Capra ibex ibex*) have been shown to exhibit unusually high survival to relatively advanced ages (> 10 years), leading to speculation that males may engage in an energetically conservative reproductive strategy that increases survival. We investigated the extent to which the adoption of alternative mating tactics contributes to the extraordinary survival of adult males in this species. Because basic information on the mating system of Alpine ibex is scarce, we first characterized the temporal and spatial distribution of receptive females. Our observations during 3 consecutive rutting seasons revealed 2 alternative mating tactics. Apparently dominant males monopolized individual, receptive females by following and defending them, a tactic known as 'tending'. In contrast, apparently subordinate males tried to achieve temporary access to tended females when the latter started to run, a tactic referred to as 'coursing'. In total, 24 copulations were observed, of which 20 (83.3%) were the result of tending and 4 were the result of coursing. The adoption of the 2 tactics was strongly age-dependent; older males (9-12 years) engaged primarily in tending, while younger males (2-6 years) engaged mainly in coursing. Males adopting the coursing tactic spent more time in low-cost and less time in high-cost behaviors than males adopting the tending tactic. Time budget comparisons with another ungulate species suggested that while tending is a relatively costly tactic coursing is a low-cost tactic that may contribute to the exceptional adult survival in male Alpine ibex.

Key-words.— Alpine ibex, *Capra ibex,* life-history, mating tactic, reproductive effort, reproductive success, sexual selection, survival

INTRODUCTION

Sexual selection is expected to favor the evolution of alternative male mating tactics when the variance in male fitness is high (Emlen and Oring 1977; Shuster and Wade 2003). This is usually the case when receptive females are aggregated in space but show asynchronous sexual receptivity. Under these conditions, a subset of males may be able to monopolize multiple receptive females, thereby excluding other males from mating. In polygynous ungulates, common male tactics to monopolize 1 or more receptive females are the direct defense of potential mates (Clutton-Brock et al. 1982; Hogg 1987) or the defense of territories on which females reside (Carranza et al. 1990; Clutton-Brock et al. 1988; von Hardenberg et al. 2000). The successful defense of females or territories is usually restricted to a small number of fully-grown and therefore older males (Isvaran 2005; Wolff 2008).

Other, often younger males must resort to alternative reproductive tactics, including abducting estrous females or sneaking copulations when the opportunity arises (e.g., ‘kleptogamy’ in red deer, *Cervus elaphus,* Pemberton et al. 1992; ‘coursing’ in bighorn rams, *Ovis Canadensis,* Hogg 1987), in order to achieve reproductive success.

The observation that alternative mating tactics are often age-dependent (Isvaran 2005; Wolff 2008) may have far reaching consequences for the life history of a species. Members of long-lived, iteroparous species must decide during each breeding season how much energy to invest in current reproduction versus future survival in order to maximize their lifetime reproductive success (Clutton-Brock 1984; Krebs and Davies 1995). Because reproductive costs and benefits may vary greatly among alternative tactics (Clutton-Brock et al. 1982; Moore et al. 1995; Pelletier 2005; Saunders et al. 2005), the age-dependent adoption of different mating tactics is likely to be a crucial determinant of reproductive success and age-specific survival (see also (Loison et al. 1999a).

The Alpine ibex (*Capra ibex ibex*) is a sexually highly dimorphic mountain ungulate. The mating system of this species is poorly known (i.e. Aeschbacher 1978). A recent study by Toïgo et al. (2007) revealed that, under good environmental conditions, adult male Alpine ibex survived to the advanced age of 10-13 years, with a yearly survival rate of 96-98% (Toïgo et al. 2007). Under poor conditions, survival remained high among males aged 2-8 years but dropped to 85% among males aged 8-13 years. Overall, adult male survival exceeded the survival of other large herbivores by 5-20%. In comparison, yearly survival of male bighorn sheep aged 2-8 years was less than 85% (Bonenfant et al. 2009). Since age-specific mortality patterns among polygynous males are thought to be closely linked to reproductive effort during the mating season (Festa-Bianchet et al. 2000; Stevenson and Bancroft 1995; but see McElligott and Hayden 2000), these findings suggest that male Alpine ibex pursue a comparatively conservative life history strategy, leading to questions as to whether the age-dependent adoption of alternative mating tactics by male Alpine ibex contributes to their exceptional survival.

To explore this idea, we characterized the mating system of Alpine ibex, with particular attention given to age-related differences in the tactics that males use to compete for females. We present data on the spatial distribution and reproductive cycle of female ibex, both of which contribute to the ecological conditions under which discontinuous mating behaviors are likely to evolve (Shuster and Wade 2003). Based upon work by Aeschbacher (1978) as well as comparative data from other ungulates, we predicted that male Alpine ibex should engage in at least 2 different mating tactics - one in which mostly older males try to monopolize receptive females (tending) and a second in which mostly younger males try to achieve temporary access to tended females (coursing). Taking the survival analyses by Toïgo et al. (2007) into account, we expected the latter to be a relatively low-cost tactic that should involve fewer high-cost and more low-cost activities than defending females. In addition to providing the first detailed description of the mating system of Alpine ibex, our analyses yield intriguing insights into relationships among mating tactics, energetics, and survival in polygynous ungulates.

MATERIALS & METHODS

Study population.— The study was carried out in the lightly hunted 'Cape au Moine' population of Alpine ibex north of the village of Les Diablerets (VD) in the Swiss Alps (46° 22' N; 07°09' E, 1700-2550 m). The study area, which measured approximately 13.2 km^2, consisted mainly of a steep west to east mountain ridge that was characterized by extensive open alpine pastures at higher altitudes (> 1800 m) and by patches of dense spruce forests (*Picea abies*) at lower altitudes (< 1800 m). It was interspersed with rocky cliffs of varying size. Throughout the winter, the north side of the ridge remained covered by snow while substantial portions of the south side were often free of snow due to solar radiation and avalanches.

Females with young lived year-round in groups of up to 50 animals that were permanently resident in the study area. In contrast, males formed loose groups of variable composition (see also Villaret and Bon 1998) and at least some males roamed between the study population and two adjacent populations. This roaming behavior is also known from other ibex populations (Abderhalden 2005) and seems to be particularly apparent during the pre-rut period in November-December (see also Parrini et al. 2003). In late autumn and winter (i.e. during the rut), the animals primarily inhabited the steep, south-facing mountain slopes and cliffs that were relatively free of snow, as has been reported for other populations of Alpine ibex (Grignolio et al. 2003).

Sexual dimorphism and life history of Alpine ibex.— Alpine ibex are sexually dimorphic, with adult males being more than twice as heavy (95 kg versus 45 kg, Loison et al. 1999b) and possessing much larger horns than adult females (>90 cm versus >30 cm, Lüps et al. 2007). Compared to other ungulates, male Alpine ibex display a rather slow yearly growth. As a consequence, body weight does not become asymptotic until the age of 8-9 years, peaking at 11 years of age (Lüps et al. 2007). In contrast, in bighorn sheep and red deer, body weight becomes asymptotic at the age of 6 years (Mysterud et al. 2001; Pelletier and Festa-Bianchet 2006); in Alpine chamois, *Rupicapra rupicapra*, another polygynous mountain ungulate, this occurs by the age of 4 years (Bassano et al. 2003). Male Alpine ibex exhibit an exceptionally good adult survival up to 8 years of age, and, under good conditions, up to 13 years of age, thereby exceeding adult survival rates for other large herbivores by 5-20% (Toïgo et al. 2007).

Observation periods and conditions.— Alpine ibex were observed between December and January of 2005-06, 2006-07 and 2007-08. This corresponds to the annual period of rut, when females in the study population were sexually receptive. Each year, rut was determined to have begun on the day when the first female was seen to engage in a prolonged association with multiple males. Observations continued for 4-8 weeks after the rut began. During data collection, 1-3 observers monitored the animals visually from dusk to dawn using spotting scopes. The distance between observers and the study subjects varied but was typically between 150 and 1500 meters. In 2005-06, observations were restricted to a part of the study area that was easily accessible and provided safe observation conditions even when the risk of avalanches was high. In the 2 following years, as snow conditions permitted, observations (with exception of the focal animal observations) were extended to the entire study site.

Identification of individuals and age determination.— In total 121 males (> 2 years old) and 30 females (> 2-3 years old) in the study population could be individually recognized based on unique characteristics of their horns and coat coloration. In addition, 30 of these animals were individually marked on both ears with colored and numbered ear tags. 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.

The age of male Alpine ibex was determined by counting the conspicuous annuli on the outer side of the horns (Ratti and Habermehl 1977). In animals that were captured, found dead, or were killed by hunters, this could be done at close distance. For free-ranging unmarked and unknown males, age estimation was carried out directly during observations in the field; for free-ranging unmarked but known (photo-identified) individuals, estimations were performed retrospectively by inspecting all available photographs of these animals. While the reliability of age estimation for unknown animals could not be quantified, this was possible for some of the known males. Accordingly, the ages of 33 males were first estimated from photographs and later confirmed through direct inspection; in all cases, both aging methods yielded the same results, suggesting that age determination for free-ranging male Alpine ibex via photographs is reliable. All aspects of animal capture and data collection were approved by the Swiss Federal Office of the Environment (FOEN) and the Swiss Federal veterinary office

(FVO) and conformed to guidelines established by the American Society of Mammalogists (Gannon and Sikes 2007).

Sampling methods.— During all 3 years of the study, daily animal censuses were carried out to collect information on the size and sex-age structure of the population. Because the whole study area was too big to be monitored within 1 day, population-wide censuses were composed of 2 censuses performed on consecutive days.

To obtain data on male activity budgets each day observers selected 1-3 known males as focal animals, which were then observed continuously for as long as possible (Altmann 1974). The behaviors recorded included feeding (snout in contact with vegetation), standing, moving (walking and running), and lying down. In addition, multiple courtship behaviors displayed by males were registered, including low-stretch (neck straightened and head held in-plane with the back with the muzzle pointed towards a female), tongue-flick (flicking with tongue towards a female), sniff (sniffing a female, or the site where a female had urinated), lick (licking a female), flehmen (lifting upper lip after having sniffed a female or the site where a female had urinated), touch (touching a female with the snout), masturbation (touching penis with snout while standing next to a female), scent-urination (urinating on front legs while standing next to a female), mount attempt (raising front half of body to mount a female), mount (placing the sternum on the female’s back), and copulation (subset of mounts in which the abdomen of the male is firmly pressed against the vulva of the female, resulting in a supposed intromission of the penis). Finally, several agonistic behaviors among males were recorded, including evasion (walking away from an approaching male), flight (running away in response to an approaching male), displacement (driving another male away by slowly approaching it), chase (pursuing another male at high speed), rush (running towards another male, usually with slightly lowered horns), horn contact (locking horns with those of another male), horn clash (hitting the horns against those of another male), and homosexual mount (mounting another male). The activities feeding, standing and lying down were summarized based on their supposed positive effects on the energetics of animals in the category of ‘low-cost’ behaviors, whereas moving and the various courtship and agonistic behaviors, which can be regarded as energy intensive investments into reproduction, were pooled in the category of ’high-cost’ behaviors.

In 2005-06, focal observations were also conducted on females tended by males to determine (1) which males were associated with the female, (2) the number of mount attempts, mounts, and copulations each female received, as well as (3) the number of times a female ran away from males.

To obtain information on how males gained and maintained access to receptive females, in each year, all instances were recorded in which a female was attended by ≥ 2 males (of which one was the tending male) for at least 10 minutes. These females were scanned between 1 and 19 times a day (mean ± SD = 4.1 ± 3.5 scans per day, N = 211 females) to record the IDs, ages and mating tactics of all associated males, as well as to estimate the distances (in female body lengths: FBL) between the female and associated males. The 10-min observation period appeared to be sufficient to distinguish between non-receptive females that were only briefly approached by males (presumably to check their estrous status) and receptive females that were focus of prolonged attention by males. Ad libitum sampling was used to record all observed mount attempts, mounts and copulations performed by males.

Data analysis.— A Wilcoxon matched pairs test was used to compare the distance to receptive females for males that simultaneously attended the same female but displayed different mating tactics (Sheskin 2004). Because attended females were scanned multiple times per day (resulting in multiple male-female distances for the same pair of animals), mean values per female and day were used for this test.

To examine differences in the activity budgets of individual males as a function of age and the mating tactic adopted, mixed-effects models using restricted maximum likelihood method (REML) were employed, with animal ID and year of observation as random factors and mating tactic and age as fixed effects (Crawley 2007). To investigate the relationship between individual male age and mating tactic, the proportion of time a male spent in the different mating tactics was calculated. REML mixed-effects models were then fitted with age as a fixed effect and animal ID and year of observation as random effects. For all of these analyses, only focal observations lasting > 30 mins were used. Prior to analyses, the proportion of time spent in each activity or male ~~tactics~~ was arcsine square-root transformed to approximate a normal distribution (Zar 1999). Residuals for the REML models were normally distributed.

Binomial tests were conducted to examine differences in the number of mounts and copulations by males that adopted different mating tactics (Sheskin 2004). To explore the effect of male age on the frequency of each mating tactic, we compared the ages and mating tactics of males associated with attended females. Because these females were scanned multiple times per day, only the first observation per day per female was used to avoid pseudo-replication. Frequency distributions of the observed mating tactics were calculated for each age class (year) of males and generalized additive models with Poisson errors were used to assess potential behavioral differences between age classes (Crawley 2007).

To account for the possibility that age-dependent frequency distributions were influenced by the number of males present in the different age classes (i.e. by the male age-structure of the population each year), we calculated a standardized tactic index, S_i, which represented the average contribution of an individual of a specific age class i to the frequency of different mating tactics. This was done using the formula:

$$S_i = O_i/(N_i \times \sum (O_i/N_i))$$

where O_i is the observed frequency of the tactic in the age class i and N_i is the average number of males in the age class i present during that season. The standardized values S_i of the different age classes i were then averaged over the 3 years of the study. Generalized additive models were used to test for age effects on the resulting averaged standardized values (Crawley 2007).

RESULTS

Population size and structure.— Censuses of animal numbers during the rutting seasons in 2006-07 and 2007-08 indicated that population size varied between 220 and 270 animals, with an adult (age ≥ 1 year) sex ratio of 0.62-0.77 males per female (Table 1). The number of males per age class showed a general trend to decline with increasing age (Fig. 1); oldest males aged 12, 13 and 14 years in the three seasons, respectively.

Spatial and temporal distribution of receptive females.— During all 3 years of the study, female Alpine ibex showed a patchy spatial distribution during the rutting season, with females distributed in small aggregations containing 1-20 individuals (Fig. 2). Distances between aggregations were typically less than a few hundred meters, permitting individual males to move between adjacent groups of females within a few minutes.

A total of 211 females were observed that were attended by multiple males during the study. The dates on which the first female associations were recorded were December 9, 5 and 13 in 2005, 2006, and 2007, respectively. During the rut in 2005-2006, observations were spread over 48 days; 69.8 % of observed mating associations occurred in the first 2 weeks after the beginning of the rut, with 86.7 % and 98.1 % of mating associations completed by weeks 4 and 5, respectively. The frequency of associations peaked during week 2, when 43.3 % of all associations were observed. The same general pattern was observed in the 2 subsequent years, when observations continued for 38 and 29 days after the beginning of the rut.

Daily scans of male-female associations indicated that female alpine ibex were of interest to males for only a brief period of time. Thus, only 4 out of 27 (15%) individually identifiable females were in association with males for ≥ 2 consecutive days. Five identifiable females were observed associating with males at 2 different times within a single rutting period; the interval between successive associations by these females were 18 and 21 days, suggesting that these females may have undergone 2 rounds of sexual receptivity.

Qualitative description of observed mating tactics.— Our observations confirmed that during the rut, male Alpine ibex adopted 2 different mating tactics to gain access to receptive females: one tactic, called ‘tending’, was adopted by apparently dominant males, while the other tactic, called ‘coursing’, was adopted by apparently subordinate males. Tending males consistently followed individual females with which they were associated and which they courted intensively. Typically, a tending male had exclusive access to a female (Fig. 3) and would defend her against competitors, usually via short displacements, if other males attempted to approach the female. In contrast, coursing males did not have free access to receptive females. Only if a physical obstacle separated the tending and the coursing male did the latter approach the female without being immediately displaced. Normally, however, coursing males remained some meters distant from the female and her tending male (Fig. 3). When the female started to run, all associated males (tending and coursing) ran after her (Fig. 4), with the coursing males trying to bypass the tending male to mount the female, often while running (see below). Coursing males were never observed to initiate such chases. That is, they never drove the female away from the tending male as long as the female and tending male were standing close together nor did they attempt to engage the tending male in a fight. Instead, coursing males always waited for the female to move or run away from the tending male before engaging in pursuit. These tactics were not fixed and individual males were seen to switch between tending and coursing both within and between seasons.

Number and spatial distribution of associated males.— No more than 1 male at a time was observed to tend a female at a given point in time. The number of coursing males per female ranged from 1-10, with a median of 3.0 males per female (inter-quartile range: 2.0-3.75). Tending males were typically located significantly closer (1.16 FBL) to females than the nearest coursing male (5.0 FBL; inter-quartile ranges: 0.83-2.00 and 3.50-7.0, respectively; N = 197, Z= 11.91, P < 0.0001).

Activity budgets while tending and coursing.— During the 3 annual rutting periods, a total of 786 hrs of focal observations were completed on 57 different males; the mean (± SD) duration of each focal observation session was 5.0 ± 2.0 hrs, yielding a mean of 13.8 ± 11.3

hrs of observation per focal animal. The REML mixed-effects model showed that, when coursing, males allocated an overall greater percentage of their time to low-cost behaviors (i.e. feeding, standing and lying) than they did when they were tending (85.4 ± 11.6% vs. 52.1 ± 28.9%). In contrast, the overall percentage of time spent in high-cost behaviors (i.e. courtship and agonistic behaviors and moving) was greater while tending than while coursing (45.1 ± 29.9% vs. 14.3 ± 11.7%). Age had no significant effect on the percentage of time allocated to either of these categories of behavior (Table 2).

Mounts and copulations.— A total of 81 mounts (including 24 copulations) were recorded for the 211 females tended during this study. Thirty-one of these mounts involved a single female who was the recipient of 27 mounts by at least 7 different males within a period of 19 minutes. The behavior of this female, specifically her slow movements and lack of effort to escape approaching males, suggested that she was injured and thus we excluded this female from all subsequent analyses of mounting and copulation behavior.

Of the remaining 210 females, 13 were seen to engage in copulations; 20 of these copulations were with tending males, while 4 were with coursing males ($N_{tend} = 20$, $N_{course} = 4$; Binomial test, $P = 0.002$). None of these females copulated with more than 1 male. On average, each female engaged in 1.7 ± 1.0 copulations. Of the 50 mounts recorded (involving 21 different females), 30 were by tending males while 20 were by coursing males ($N_{tend} = 30$, $N_{course} = 20$; Binomial test, $P = 0.203$). Two females were mounted by 3 different males while 5 were mounted by 2 different males; all of the remaining females were mounted by only a single male. On average, each female engaged in 2.3 ± 1.4 mounts.

Analysis of 144 hrs of continuous focal observations on 32 tended females (4.2 ± 2.5 hrs per tended female) monitored during 2005-2006 indicated that females received 0.22 mounts and 0.05 copulations per hr while being tended. During the same focal observations, 102 instances were recorded in which a female ran in front of (i.e. was pursued by) the males for at least 5 seconds, which corresponds to 0.7 runs per hr while being tended. On 18 occasions during these runs, males attempted to mount the female; these attempts resulted in 11 mounts. Thus, tended females received 0.18 mount attempts and 0.11 mounts per run. All observed mount attempts and mounts recorded during runs were performed by coursing males. Tending males never tried to mount a female during a run; this difference between tending and coursing males was significant (mount attempts: $N_{tend} = 0$; $N_{course} = 18$; Binomial test, $P < 0.0001$). Coursing males conducted 11 (79%) of their 14 total observed mounts during runs; the other 3 mounts occurred when the female was standing still, but at a relatively large distance from the tending male.

Age-dependent adoption of mating tactics.— Age had a considerable effect on the mating tactic adopted by individual males during the first 4 weeks of the rut, when the majority of instances of tending females were recorded. The REML mixed-effects model showed that the proportion of time spent coursing decreased with increasing male age (Table 3). Closer inspection of the data revealed, however, that the proportion of time spent coursing increased until the age of 4 years; only after that age did the proportion of time spent coursing decline (Fig. 5). Males aged 10-13 years devoted only small proportion of their time to this tactic. The apparent increase in coursing for age class 14 years was due to a single male that spent a large proportion of time coursing during 1 day of observation. In comparison, the percentage of time spent tending increased significantly with male age (Table 3). Males ≤ 4 years devoted almost no time to the tending tactic. The proportion of time spent tending peaked between 9 and 11 years of age, while a marked decrease became apparent thereafter (Fig. 5).

At the population level, generalized additive models demonstrated that the frequencies with which the tending and coursing tactics were observed varied significantly with male age (tending ~ s(Age): d.f. = 6.9, Chi-square = 77.4, $P > 0.0001$; coursing ~ s(Age): d.f. = 7.7, Chi-square = 297.8, $P > 0.0001$; Fig. 6). Coursing was displayed primarily by males $\leq$ 7 years of age; collectively, these animals accounted for 90% of all observations of coursing. Conversely, males ≥ 7 years accounted for about 95.7% of all observed episodes of tending. Among the older males, the age classes 10 and 11 years accounted for 57.8% of the observed tending events while males ≥ 12 years represented only 9.0% of tending episodes.

The effects of age on the observed mating tactics remained significant when the number of males per age class was taken into account (standardized tending index ~ s(Age): estimated d.f. = 4.4, F = 10.0, $P = 0.002$; standardized coursing index ~ s(Age): estimated d.f. = 4.2, F = 3.7, $P = 0.044$). Hence, the standardized index for the tending tactic was very low for all age classes $\leq$ 6 years (Fig. 7). A steady increase could be detected for age classes of 7-12 years of age, with a marked decline thereafter. The standardized coursing index, however, was highest for age classes of 3-6 years and lowest for age classes of 8-13 years. Collectively, these findings suggest that male reproductive tactics are strongly influenced by male age.

DISCUSSION

As in other seasonally breeding ungulates inhabiting alpine environments (e.g., red deer: Clutton-Brock et al. 1982; Alpine chamois: Willisch and Ingold 2007), mating activity in Alpine ibex spread over more than 4 weeks per year. Receptive females were only moderately temporally synchronized and showed a patchy spatial distribution in the study area, leading to a high level of intra-male competition for access to mates. The 2 alternative male mating tactics documented in the study population – tending and coursing – bear a strong resemblance to mating tactics previously reported for bighorn sheep (Hogg 1987, 1984), mountain goats, *Oreamnos americanus* (Mainguy et al. 2008) and feral goats, *Capra hircus* (Saunders et al. 2005). Our observations indicate that both tactics resulted in mating opportunities, although mating success in the form of copulations was higher for the tending tactic. In our study population, the adoption of alternative mating tactics was strongly age-dependent, similar to findings for other polygynous ungulates with alternative mating tactics (Mainguy et al. 2008; Saunders et al. 2005). Tending was most common among older males, while coursing was most pronounced in younger males. Interestingly, regardless of age, the proportion of time that individual males spent in low-cost behaviors (i.e. feeding, standing and lying) was greater for coursing than for tending while the opposite was true for high cost behaviors (i.e. moving and social behaviors).

Considering the spatial and temporal distribution of receptive females in our population, the high level of intra-male competition, and the presumably strong sexual selection associated with these conditions (Shuster and Wade 2003), it is not surprising that males in the population engaged in alternative mating tactics. The finding that individual male Alpine ibex of all ages switched between tactics within the same rutting period is in accordance with other species with similar mating systems (e.g., bighorn sheep: Hogg 1987; feral goats: Saunders et al. 2005) and suggests that these tactics represent a behavioral polyphenism within Alpine ibex. In contrast to other mating phenotypes (i.e. developmental or genetic polymorphisms), behavioral polyphenisms are characterized by frequent and rapid reversibility (Shuster and Wade 2003). As a result, individual males have the potential to respond quickly to changing mating conditions to maximize their reproductive success.

At the same time, however, our study demonstrated that male age had strong effect on which mating tactic an individual adopted. This was evident not only at the individual level (proportion of time individuals spent in each tactic), but also at the level of the population (overall frequency with which each tactic occurred). Accordingly, tending was adopted primarily by older males aged 9 to 12 years. Coursing, on the other hand, was adopted mainly by males ranging from 2 to 6-7 years of age. These patterns are in general consistent with data from other polygynous ungulates in which mating tactics are size- and / or weight-dependent and therefore also age-dependent (Isvaran 2005; Wolff 2008). To establish and maintain access to receptive females by tending, usually high dominance status (see also Hogg 1984; Mainguy et al. 2008; Saunders et al. 2005) and therefore a generally large body-size is required (Decristophoris et al. 2007). Because body-size in male Alpine ibex increases steadily with age up to about 8-9 years (Lüps et al. 2007), it is reasonable to assume that only older, fully grown males are able to apply the tending tactic successfully. In contrast, agility and running speed are likely to be the crucial qualities of successful coursing males (Coltman et al. 2002; Hogg and Forbes 1997), since these animals must catch up with running females to copulate. Agility in male Alpine ibex is likely to be negatively weight- and size- dependent and, hence, coursing in this species (as in other polygynous ungulates with comparable mating tactics; Hogg and Forbes 1997; Saunders et al. 2005) should be more common among younger males. Interestingly, the average standardized tending indices (which estimated the contribution to the recorded tending events while taking into account the number of males per age class) for the 2 oldest age classes (13 and 14 years) were noticeably reduced compared to the slightly younger age classes, suggesting that these males might have passed their peak of reproductive performance and were showing signs of senescence.

Although coursing males did not have free access to receptive females, they were capable of making use of sudden mating opportunities, as shown by the observed coursing mounts and copulations. To succeed, coursing male Alpine ibex had to rely on the behavior of the female; these males did not try to create mating opportunities but instead waited for the female to move or run away from the tending male. Coursing males in other species, such as bighorn sheep and feral goats, are known to actively initiate chases of receptive females either by overt aggression against the tending male or by driving away the female (Hogg 1984; Saunders et al. 2005). In comparison, coursing male Alpine ibex were relatively passive and made only opportunistic use of mating opportunities that arose as a result of female behavior. This less active role in coursing may help to explain the relatively low rates of mounts and copulations detected during this study. Receptive females in the study population engaged in on average only 0.05 copulations per hr tended; in contrast, female bighorn sheep (in which males take a more active role in initiating coursing) engage in 1-2.5 copulations per hr (data derived from Hogg and Forbes 1997). According to Hogg (1988), individual bighorn ewes experienced up to 60 copulations during one estrous period; in contrast, individual female Alpine ibex engaged in an average of less than 2 copulations per estrous.

Our behavioral observations strongly suggest that both mating tactics displayed by male Alpine ibex may lead to mating success, although only about 1 in 6 copulations were performed by coursing males. In contrast, the number of copulations by coursing male bighorn sheep, which are known to sire > 40% of the lambs (Hogg and Forbes 1997), was nearly equal to the number achieved by tending males (Hogg 1988). Whether coursing Alpine ibex can attain levels of reproductive success similar to those for coursing male bighorn (Hogg and Forbes 1997) or Soay sheep (*Ovis aries*; Coltman et al. 1999) remains unknown. Although the low proportion of copulations observed for coursing male Alpine ibex suggests that this is unlikely genetic analyses of paternity are required to determine actual reproductive success of coursing versus tending males in this species.

Assuming that spending more time in energy consuming behaviors contributes negatively to the energy balance of animals (Pelletier 2005; Willisch and Ingold 2007), our analyses of time budgets suggest that coursing is energetically less expensive than tending and that the energetic difference between these tactics may be particularly pronounced in Alpine ibex. Accordingly, while coursing male Alpine ibex allocated on average 84.5% of their time to, so called, low-cost and only 14.3% to high-cost behaviors. In comparison, coursing male bighorn sheep spent only about 61% of their time in low-cost behaviors while the high-cost behaviors accounted for remarkable 37% (data derived from Pelletier 2005). Since male mortality in ungulates inhabiting temperate climates is thought to depend greatly on rut-related investments in reproduction (Toïgo and Gaillard 2003) the adoption of a low-cost tactic is expected to enhance the survival of their users. Hence, male Alpine ibex engaging in the coursing are likely to enjoy high survival without foregoing the possibility of participating in reproduction. As predicted, the age-dependent adoption of the opportunistic low-cost tactic coursing could, therefore, contribute to the consistently high survival found among male Alpine ibex up to 8 years of age.

On the other hand, given that coursing was only rarely adopted by males ≥9 years of age, the high survival rates of about 85-96% (depending on the ecological conditions) among 8-13 years old males cannot directly be attributed to the low-cost tactic coursing. Neither can they be explained by an energetically favorable tending tactic, as this tactic appears to incur high energetic costs in male Alpine ibex. Accordingly only 45.1% of the tending time was devoted to low-cost behaviors, whereas time spent in high-cost behaviors constituted 52.1%. Tending male bighorn sheep, in comparison, spent with about 78% much more of their time in low-cost behaviors and correspondingly much less time (about 22%) in high-cost behaviors (data derived from Pelletier 2005), suggesting that the costs of tending are higher in Alpine ibex. Still, yearly survival for male bighorn sheep did not exceed 80% when they reached their peak in breeding activity with 5-8 years of age (Bonenfant et al. 2009).

Considering that the environment-related decline in survival detected by Toïgo et al. (2007) involved largely the same age classes that participated most actively in rutting and that made most extensive use of the tending tactic our results suggest that the rut-related behavior, nevertheless, plays an important role in the survival and the energetics of Alpine ibex. Another possible mechanism adding to the good survival of older males might, therefore, be the reduction of energy-intensive intra-male competitions as a secondary effect of the passive and less overt behavior of coursing males. Because tending males have to defend receptive females against multiple coursing competitors, they might particularly profit from the fact that the latter do not use overt aggression to attain temporary access to defended females. As a consequence, tending male Alpine ibex might be able to significantly cut down on costly interactions, since they must not block all the time attacks by coursing males. Compared to other polygynous species in which frequency and intensity of intra-male competitions are known to culminate concomitantly with the peak in mating activity (Clutton-Brock et al. 1979), tending male Alpine ibex might experience considerable energy savings that could ultimately lead to an improved rate of survival.

Overall, our study demonstrated that the comparatively high adult survival reported previously for male Alpine ibex may result at least partially from the specific alternative mating tactics employed by males during the rutting season. In contrast to tending, coursing appeared to be a low-cost tactic that may directly contribute to the relatively good survival of the younger males which are the principal users of this tactic. Further, our observations indicate that the passive nature of coursing in this species might also confer survival benefits to older, tending males by reducing the costs associated with defending females from reproductive competitors. Future studies that quantify directly the energetic consequences of mating behavior in Alpine ibex will be valuable in demonstrating the impacts of alternative male mating tactics on the life history patterns of these animals.

ACKNOWLEDGEMENTS

We thank P. Decristophoris, I. Glanzmann, N. Grandjean, B. Nussberger and C. Wittker for their assistance in data collection. Furthermore we appreciate the help of numerous people in capturing and marking Alpine ibex, above all J.-C. Roch, M.-P. Ryser-Degiorgis and N. Marreros, as well as K. Bieri, P. Deleury, C. Hebeisen, B. Hofer, I. Leathwood, H. Nimmervoll. We thank E. Lacey, M. Festa-Bianchet, K. E. Ruckstuhl and an anonymous referee for valuable comments on the manuscript. We are particularly grateful to S. Sachot and J.-C. Roch of the Canton Vaud, as well as to R. Schnidrig-Petrig and Nicole Imesch of the Federal Office of the Environment (FOEN) who permitted and supported the conduction of this study in the population of ‘Cape au Moine’ (VD). Financial support was provided by the FOEN.

LITERATURE CITED

ABDERHALDEN, W. 2005. Raumnutzung und sexuelle Segregation beim Alpensteinbock *Capra ibex ibex*. Nationalpark-Forschung Schweiz 92.

AESCHBACHER, A. 1978. Das Brunftverhalten des Alpensteinbocks. Eugen Rentsch Verlag, Erlenbach-Zürich.

ALTMANN, J. 1974. Observational study of behavior - Sampling methods. Behaviour 49:227-267.

BASSANO, B., A. PERRONE, AND A. VON HARDENBERG. 2003. Body weight and horn development in Alpine chamois, *Rupicapra rupicapra* (Bovidae, Caprinae). Mammalia 67:65-73.

BONENFANT, C., F. PELLETIER, M. GAREL, AND P. BERGERON. 2009. Age-dependent relationship between horn growth and survival in wild sheep. Journal of Animal Ecology 78:161-171.

CARRANZA, J., F. ALVAREZ, AND T. REDONDO. 1990. Territoriality as a mating strategy in red deer. Animal Behaviour 40:79-88.

CLUTTON-BROCK, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. American Naturalist 123:212-229.

CLUTTON-BROCK, T. H., S. D. ALBON, R. M. GIBSON, AND F. E. GUINNESS. 1979. The logical stag - Adaptive aspects of fighting in red deer (*Cervus elaphus* L). Animal Behaviour 27:211-225.

CLUTTON-BROCK, T. H., D. GREEN, M. HIRAIWA-HASEGAWA, AND S. D. ALBON. 1988. Passing the buck: resource defence, lek breeding and mate choice in fallow deer. Behavioral Ecology and Sociobiology 23:281-296.

CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. 1982. Red deer. Behavior and ecology of two sexes. The University of Chicago Press, Chicago.

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.

CRAWLEY, M. J. 2007. The R book. John Wiley & Sons Ltd, Chichester.

DECRISTOPHORIS, P. M. A., A. VON HARDENBERG, AND A. G. MCELLIGOTT. 2007. Testosterone is positively related to the output of nematode eggs in male Alpine ibex (Capra ibex) faeces. Evolutionary Ecology Research 9:1277-1292.

EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and evolution of mating systems. Science 197:215-223.

FESTA-BIANCHET, M., J. T. JORGENSON, AND D. Reale. 2000. Early development, adult mass, and reproductive success in bighorn sheep. Behavioral Ecology 11:633-639.

GANNON, W. L., AND R. S. SIKES. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809-823.

GRIGNOLIO, S., F. PARRINI, B. BASSANO, S. LUCCARINI, AND M. APOLLONIO. 2003. Habitat selection in adult males of Alpine ibex, *Capra ibex ibex*. Folia Zoologica 52:113-120.

HOGG, J. T. 1984. Mating in bighorn sheep - Multiple creative male strategies. Science 225:526-529.

HOGG, J. T. 1987. Intrasexual competition and mate choice in Rocky-Mountain bighorn sheep. Ethology 75:119-144.

HOGG, J. T. 1988. Copulatory tactics in relation to sperm competition in Rocky-Mountain bighorn sheep. Behavioral Ecology and Sociobiology 22:49-59.

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.

ISVARAN, K. 2005. Variation in male mating behaviour within ungulate populations: patterns and processes. Current Science 89:1192-1199.

KREBS, J. R., AND N. B. DAVIES. 1995. An introduction to behavioural ecology, 3rd ed. Blackwell Science, Oxford.

LOISON, A., M. FESTA-BIANCHET, J. M. GAILLARD, J. T. JORGENSON, AND J. M. JULLIEN. 1999a. Age-specific survival in five populations of ungulates: Evidence of senescence. Ecology 80:2539-2554.

LOISON, A., J. M. GAILLARD, C. PELABON, AND N. G. YOCCOZ. 1999b. What factors shape sexual size dimorphism in ungulates? Evolutionary Ecology Research 1:611-633.

LÜPS, P., B. BLÖCHLINGER, P. SCHMID, AND M. ZUBER. 2007. Ontogenese und Variabilität verschiedener Körpermerkmale des Steinwildes *Capra i. ibex* im Berner Oberland (Schweizer Alpen). Beiträge zur Jagd- und Wildforschung 32:495-510.

MAINGUY, J., S. D. COTE, E. CARDINAL, AND M. HOULE. 2008. Mating tactics and mate choice in relation to age and social rank in male mountain goats. Journal of Mammalogy 89:626-635.

MCELLIGOTT, A. G., AND T. J. HAYDEN. 2000. Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*). Behavioral Ecology and Sociobiology 48:203-210.

MOORE, N. P., P. F. KELLY, J. P. CAHILL, AND T. J. HAYDEN. 1995. Mating strategies and mating success of fallow (*Dama Dama*) bucks in a non-lekking population. Behavioral Ecology and Sociobiology 36:91-100.

MYSTERUD, A., N. G. YOCCOZ, N. C. STENSETH, AND R. LANGVATN. 2001. Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence, Proceedings of the Royal Society of London, B. Biological Sciences 268:911-919.

PARRINI, F., S. GRIGNOLIO, S. LUCCARINI, B. BASSANO, AND M. APOLLONIO. 2003. Spatial behaviour of adult male Alpine ibex *Capra ibex ibex* in the Gran Paradiso National Park, Italy. Acta Theriologica 48:411-423.

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.

PEMBERTON, J. M., S. D. ALBON, F. E. GUINNESS, T. H. CLUTTONBROCK, AND G. A. DOVER. 1992. Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. Behavioral Ecology 3:66-75.

RATTI, P., AND K. H. HABERMEHL. 1977. Investigations into age estimation and age-determination of mountain ibex (*Capra ibex ibex*) in Kanton Graubunden. Zeitschrift für Jagdwissenschaft 23:188-213.

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.

SHESKIN, D. J. 2004. Handbook of parametric and nonparametric statistical procedures, 3rd ed. Chapman & Hall / CRC, Boca Raton.

SHUSTER, S. M., AND M. J. WADE. 2003. Mating systems and strategies. Princeton University Press, Princeton.

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.

TOÏGO, C., AND J. M. GAILLARD. 2003. Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? Oikos 101:376-384.

TOÏGO, C., J. M. GAILLARD, M. FESTA-BIANCHET, E. LARGO, J. MICHALLET, AND D. MAILLARD. 2007. Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. Journal of Animal Ecology 76:679-686.

VILLARET, J. C., AND R. BON. 1998. Sociality and relationships in Alpine ibex (*Capra ibex*). Revue d'écologie - La terre et la vie 53:153-170.

VON HARDENBERG, A., P. BASSANO, A. PERACINO, AND S. LOVARI. 2000. Male alpine chamois occupy territories at hotspots before the mating season. Ethology 106:617-630.

WILLISCH, C. S., AND P. INGOLD. 2007. Feeding or resting? The strategy of rutting male Alpine chamois. Ethology 113:97-104.

WOLFF, J. O. 2008. Alternative reproductive tactics in nonprimate male mammals, Pp. 356-372 in alternative reproductive tactics. An integrative approach. (R. F. Oliveira, M. Taborsky and H. J. Brockmann, eds.). Cambridge University Press, Cambridge.

ZAR, J. H. 1999. Biostatistical Analysis, 4th ed. Prentice-Hall, London.

FIGURES

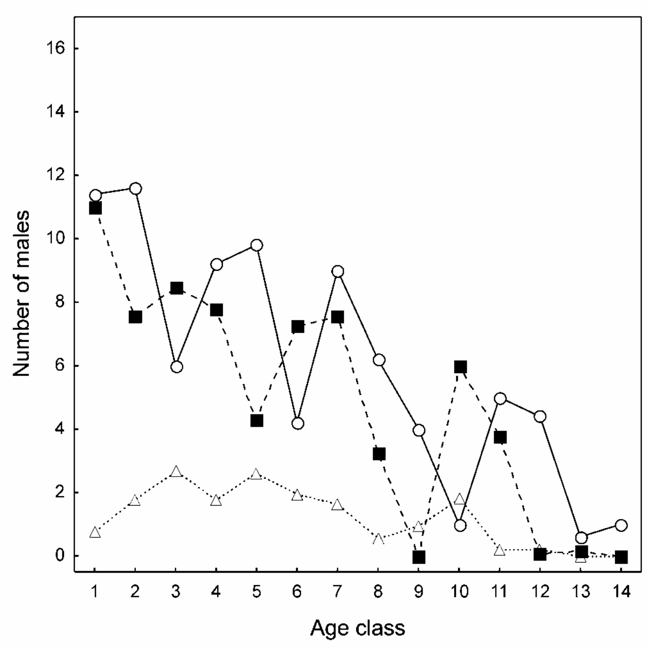

Fig. 1.— Male age structure in study area during the rutting periods in 2005-06 (open triangles), 2006-07 (filled squares) and 2007-08 (open circles), respectively. In 2005-06, only a part of the study population was monitored.

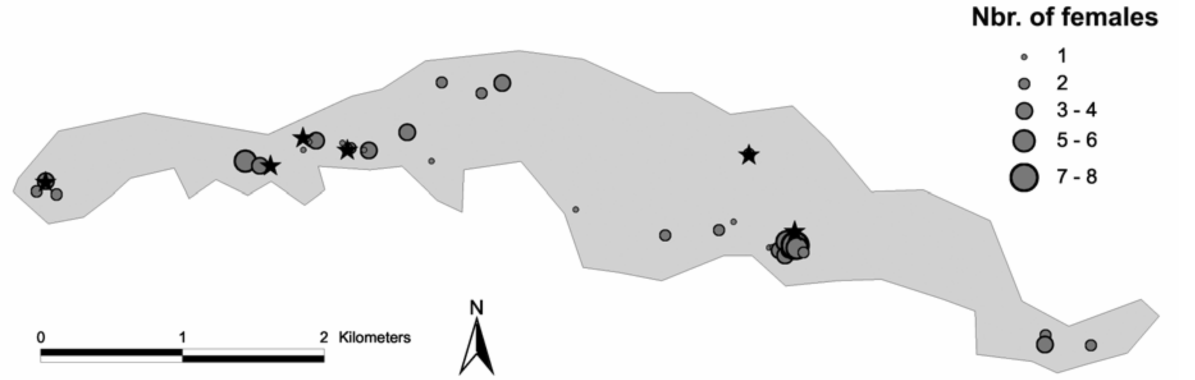

Fig. 2.— Sample spatial distribution of adult female alpine ibex on the study site during the rutting period. Data are from animal censuses performed on December 20 and 21 in 2006. The size of each circle denotes the number of females in that aggregation; stars indicate groups containing a receptive female during the censuses.

Fig. 3.— A female Alpine ibex (lying on rock) being tended by 1 male (next to female), with 3 other coursing males in close proximity (foreground). Photo by C. S. Willisch.

Fig. 4.— Five male alpine ibex pursuing a receptive female. The female is the animal furthest to the right. The tending male is the animal furthest to the left. The remaining animals are coursing males; these males often attempt to mount females during such chases. Photo by I. Glanzmann.

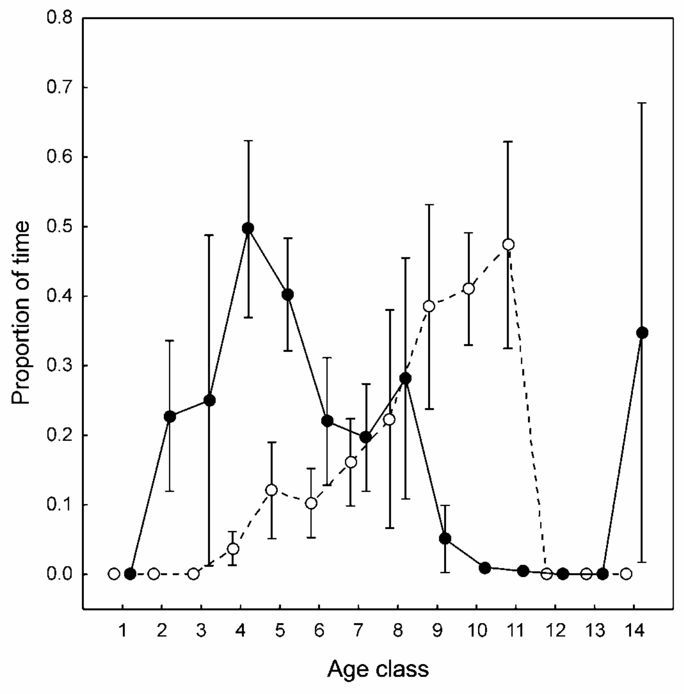

Fig. 5.— Mean (±SE) proportion of time that male alpine ibex spent tending (open circles, dashed line) versus coursing (filled circles, solid line) as a function of age class.

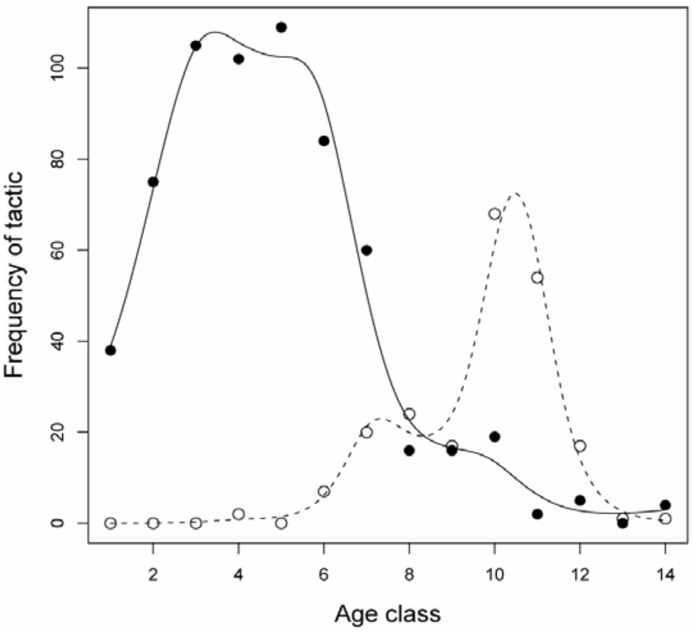

Fig. 6.— Frequency distributions of the observed tending (open circles, dashed line) and coursing males (filled circles, solid line) as a function of age class. Lines are fitted smooth curves predicted by the generalized additive models (for details see text).

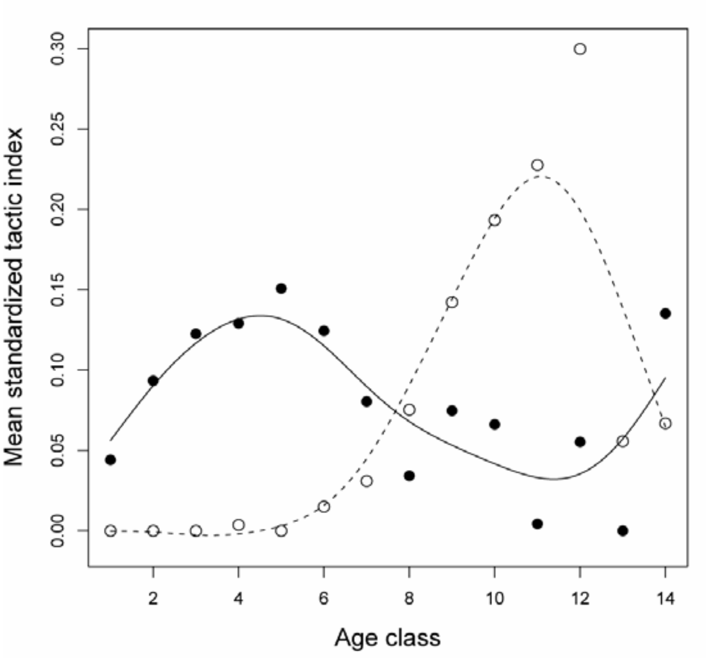

Fig. 7.— Mean standardized tending (open circles, dashed line) and coursing (filled circles, solid line) indices as a function of the age class. Lines are fitted smooth curves predicted by the generalized additive models (for details see text).

TABLES

Table 1: Animal numbers (mean ± SD; maximum) and sex ratios (mean ± SD) in the study area. Data are from animal censuses conducted during the rutting seasons in 2005-06, 2006-07 and 2007-08.

Year	N	Females	Males	Kids	Total	Sex ratio (m/f)
2005-06[a]	38	29.1 ± 7.8; 40	17.3 ± 6.0; 29	11.2 ± 3.4; 17	57.6 ± 14.5; 78	0.62 ± 0.19
2006-07[b]	13	89.6 ± 10.9; 111	67.8 ± 9.5; 81	36.6 ± 3.8; 42	194.8 ± 21.2; 221	0.76 ± 0.10
2007-08[b]	5	109.4 ± 9.6; 120	84.4 ± 6.5; 95	61.0 ± 2.5; 63	255 ± 13.23; 266	0.77 ± 0.09

a: Only a part of the population monitored.

b: Whole population monitored. Because of the size of the study area animal censuses spread over two consecutive days with safe snow conditions explaining the small sample sizes.

Table 2: Effects of age and tactic (coursing and tending) on the proportion of time that male Alpine ibex spent in low-cost and high-cost behavior as a function of the mating tactic adopted. REML mixed-effects model: Behavior ~ Tactic + Age + Animal ID + Season.

	Factor	Effect size	SE	d.f.	t-value	P-value
Low-cost behavior	Age	0.017	0.012	52	1.42	> 0.1
	Tactic	0.429	0.057	53	7.57	< 0.001
High-cost behavior	Age	-0.020	0.012	52	-1.68	< 0.1
	Tactic	-0.410	0.058	53	-7.04	< 0.001

Intercepts and random effects Animal ID and Season not shown.

Table 3: Effect of age on the proportion of time spent tending and coursing by male Alpine ibex. REML mixed-effects model: Tactic ~ Age + Animal ID + Season.

	Factor	Effect size	SE	d.f.	t-value	P-value
Tending	Intercept	-0.074	0.163	59	-0.45	0.65
	Age	0.049	0.016	59	3.14	< 0.01
Coursing	Intercept	0.809	0.124	59	6.50	< 0.001
	Age	-0.066	0.016	59	-4.12	< 0.001

Random effects Animal ID and Season not shown.

CHAPTER 2

SOCIAL DOMINANCE AND CONFLICT REDUCTION IN MALE ALPINE IBEX (*CAPRA IBEX*) DURING THE RUT

Christian S. Willisch & Peter Neuhaus

Submitted

Corresponding author:
Christian S. Willisch
Department of Eco-Ethology, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2009 Neuchâtel, Switzerland
Email: willichristian@yahoo.com

Running title:
Social dominance in rutting male Alpine ibex

Print title:
SOCIAL DOMINANCE AND CONFLICT REDUCTION IN MALE ALPINE IBEX (*CAPRA IBEX*) DURING THE RUT

Authors:
Christian S. Willisch(1) and Peter Neuhaus(1,2)

Addresses:
1) Department of Eco-Ethology, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2009 Neuchâtel, Switzerland
2) Department of Biological Sciences, University of Calgary, 2500 University Dr. NW, Calgary AB, T2N 1N4, Canada

Abstract

In polygynous ungulates high male mortality is thought to be linked to excessive energy expenditures during the rut. In Alpine ibex (*Capra ibex*) adult males show however, an unprecedented high survival. Because male Alpine ibex live in social groups we, assumed that they might reduce energy-intensive interactions during the rut by establishing strict dominance hierarchies early on. To evaluate this, we studied social interactions and mating behaviour in a population of Alpine ibex in the Swiss Alps. In accordance with our hypothesis, and in contrast to other polygynous ungulates, male Alpine ibex decreased the time spent in agonistic interactions and the number of horn fights during the rut compared to the pre-rut. Changes between access-holding males occurred always without foregoing horn fights and were entirely based on pre-established, stable dominance relationships. Hence, dominant males always gained and hold 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 oestrus females. They behaved extremely reluctant towards dominants, as they made never use of overt aggression to challenge them or to create actively transient mating opportunities. Our study supports the hypothesis that costly intra-male interactions are reduced during the mating season in Alpine ibex by the adherence to pre-established and stable dominance relationships. Accordingly, male Alpine ibex appear to be able to cut down on energy-expenditures, what in turn is likely to contribute to their superior survival.

Keywords

Aggression, dominance, mating behavior, social system, survival, ungulate

Introduction

In sexually dimorphic, polygynous ungulates, adult males generally show relatively poor survival compared to females (Toïgo and Gaillard 2003). This discrepancy between females and males results presumably, apart from higher susceptibility of males to nutritional stress and predation, from different reproductive strategies (Toïgo et al. 2007). Male mortality is commonly assumed to be higher than female mortality because males have to invest much of their resources in the acquisition and defence of oestrous females during the mating season in order to maximize their reproductive success (e.g., McElligott et al. 2003; Mysterud et al. 2004; Mysterud et al. 2005; Pelletier 2005; Pelletier et al. 2006; Yoccoz et al. 2002). As a consequence male body condition is thought to deteriorate considerably (Clutton-Brock et al. 1982; Forsyth et al. 2005) and the risks of dying during the consecutive winter can be expected to increase (Stevenson and Bancroft 1995).

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 might not be as pronounced as their high degree of sexual dimorphism suggests. They showed that the yearly survival of adult males up to the age of 10-13 years was with 85-98% exceptionally high. As a consequence, male survival in the investigated population of Alpine ibex 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), suggesting that adult male Alpine ibex pursue an energetically conservative reproductive strategy during the rut.

Willisch & Neuhaus (in press) revealed in a recent study that in male Alpine ibex the alternative mating tactic ‘coursing’ permitted individual males to participate in the reproduction without incurring high energetic costs that would ultimately lower their chances of survival. Since this low-cost tactic was principally adopted by younger males that were out to ‘steal’ copulations from access-defending (i.e. ‘tending’) males, it was likely to contribute to the low mortality rate of the younger males. The good survival of older, mostly tending males remained, however, largely unexplained. Willisch & Neuhaus (in press), therefore, proposed another, mutually not exclusive mechanism that might explain the good survival in adult male Alpine ibex. Particularly, they hypothesized that male Alpine ibex might be able to save energy by reducing costly intra-male interactions which are ordinarily necessary to obtain or defend access to receptive females. Normally, males of polygynous species are thought to compete fiercely during the mating season to gain access to mating partners (e.g., Alvarez 1993; Apollonio et al. 1990; Clutton-Brock and Albon 1979; Clutton-Brock et al. 1979; Fryxell 1987; Hsu et al. 2005; McElligott et al. 1998; Olsson 1993; Wells 1988; Wolff 1998), resulting in high energy expenditures and increased risks of mortality. Animals engaging not or less in such energy-consuming competitions might, consequently, considerably lower their energetic energy expenditures compared to other species, and ultimately profiting from an improved survival.

Although competition for access to receptive females in polygynous ungulates can generally be assumed to escalate (Parker 1974), examples that animals may refrain from taking part in escalating interactions exist (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 given among animals of differing size / weight, fighting ability or dominance rank (Hsu et al. 2005).

Two main mechanisms are known how inferior males can avoid fights which 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., vocalisation and parallel walk: Bartos et al. 2007; Clutton-Brock and Albon 1979; 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 outcome of earlier interactions with their opponents (Hsu et al. 2005; Taillon and Cote 2006) rather than on actually performed assessments. 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, once established dominance relationships could potentially replace long-lasting aggressive interactions among them 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 likely. Accordingly, rutting male Alpine ibex might be able to cut down on time- and energy-consuming intra-male interactions by establishing strictly binding dominance relationships which render unnecessary to fight for access to receptive females. Although many behavioural studies pointed out the importance of dominance in male ungulates during the rut (Hogg 1987; Hogg and Forbes 1997; Mainguy et al. 2008; McElligott et al. 1998; Moore et al. 1995; Wolff 1998), including the Alpine ibex (Aeschbacher 1978; Willisch & Neuhaus in press), none has to our knowledge conclusively shown that obligatory dominance relationships may replace intensive agonistic interactions as assessment encounters and fights to gain and maintain access to receptive females during the rut.

In this study, we investigated if adult male Alpine ibex are able to reduce energetically costly intra-male competitions during the rut to attain access to receptive females by establishing strictly binding dominance relationships among them. We predicted that individual males should not have to engage in aggressive, potentially long-lasting and costly physical interactions to gain access to receptive females. Instead access should be entirely determined by stable dominance relationships among individual males during the rut. Considering the exceptional survival of adult male Alpine ibex (Toïgo et al. 2007), we furthermore, expected costly intra-male competition to be generally reduced during the rut compared to pre-rut. Finally, we reviewed quantitative studies regarding the temporal occurrence of intra-male agonistic interactions in relation to the peak of mating activity in other polygynous ungulates. Our study aimed not only to provide insights into how males of socially living ungulates may resolve conflicts over highly valuable resources without the necessity of escalating contests, but also how the social system of animals may ultimately affect their energetics and survival.

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 (VD) in the Swiss Alps. The study area consisted mainly of a west-east directed, steep mountain ridge which was characterized by extensive open alpine pastures at higher altitudes and by patches of dense spruce forests (*Picea abies*) at lower altitudes (< 1800 m). The whole area was interspersed with rocky cliffs of varying size. In winter the north side remained always covered with snow whereas on the south side usually substantial parts of the mountain ridge were free of snow due to solar radiation and avalanches. Population size varied between 220-270 animals (Willisch & Neuhaus in press). 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 are free to join or to leave a group (Conradt and Roper 2000). Some of the males were known to roam between this and two adjacent populations. This behaviour appeared to be particularly expressed before the onset of the rut in November / December (see also Parrini et al. 2003). In late autumn and winter, and hence also during the rut, animals inhabited mainly the steep, south-facing mountain slopes and cliffs of the study area, a behaviour also found in other ibex populations (Abderhalden 2005; Grignolio et al. 2003).

Mating system and mating tactics

In a recent study by Willisch & Neuhaus (in press) it was demonstrated that single receptive females in the study population were in association by an average of 4 up to a maximum of 11 different males. Observations revealed the existence of two alternative male mating tactics (Willisch & Neuhaus in press). 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 they moved / stood too far away from the tending male (Willisch & Neuhaus, in press). This indicates that Alpine ibex are polygynous ungulates, which are expected to exhibit a high level of intra-male competition for access to mating partners.

Sampling methods

Observations were conducted on individually marked or recognizable Alpine ibex (for details see Willisch & Neuhaus in press) between November and January in 2005/06, 2006/07 and 2007/08 using spotting scopes (20-60 x 65 / 80). Observations usually covered all daylight hours. Distances between observers and animals varied, but ranged typically between 150 to 1500 meters.

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

Furthermore, 208 females (61 in 07/08, 100 in 06/07, 47 in 05/06) associated by at least two known males (one tending and one 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 not all females could be identified individually, a portion may have been sampled multiply. Ad libitum sampling was used to record horn fights (i.e. physical interactions involving horn clashes) and other agonistic interactions between males, as well as changes in the access defending, tending male.

Definition of dominance

In accordance with Drews (1993) we referred to dominance as an attribute of agonistic interactions between two 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 that individual of a dyad ‘dominant’ which won more encounters than his opponent. As a consequence the individual that won less often was considered to be ‘subordinate’. A male was considered to be the winner of single interaction encounter when it actively displaced or mounted his opponent. Conversely, a male was considered to be the loser when it evaded his opponent, or when it was mounted by his opponent. Following horn fights the winner was determined to be the male which followed his opponent persistently, occasionally displacing and / or hooking it.

Time budget data

To compare agonistic and courtship behaviours of males during the rut with the pre-rut, we determined different periods. 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 were December 9, 5 and 13 in 2005, 2006 and 2007, respectively (Willisch & Neuhaus in press). From these dates back- and onwards we split up the time between November and January into six bi-weekly periods with two pre-rut periods and four rutting periods each.

In areas far north from the equator (like this one), seasonal changes in day length may enter biases into comparisons of activity budgets collected during different periods when time use for specific behaviours is calculated as the proportion of total observation time devoted to these behaviours (as it is usually done). This problem may be particularly pronounced for animals showing distinct differences in their behaviour between day and night, as it is the case in many ruminant species (Alpine chamois, *Rupicapra rupicapra:* Ingold et al. 1998; red deer, *Cervus elaphus*: Georgii and Schroder 1983; sheep, *Ovis sp.*: van Soest 1994). Hence, supposed changes in the proportion of time spent in specific behaviours during a day can partly or completely be due to the fact that days have become shorter or longer form one period to another. To avoid this methodical pitfall we calculated the proportion of active time (i.e. the time when an animal is not lying) spent in the different behaviours (instead of the proportion of total observation time). Because this latter estimator is not as directly affected by changes in day length, we expect it to result in more reliable comparisons between seasons. Mixed Model ANOVA was used to show differences in the behaviour between periods. Animal ID and year of observation were entered as random factors. Proportions were arcsine square root transformed to meet normality. Residuals followed a normal distribution. After Mixed Model ANOVA post hoc Fisher's LSD tests were performed to detect differences between periods.

Horn fight data

Because horn fights among male Alpine ibex were rather rare events, we pooled the number of observed horn fights of all three years for the particular periods. To test if there was a difference in the number of horn fights before and during the rut, we applied a chi-square goodness-of-fit test (Sheskin 2004). In order to control for differences due to varying observation effort in the different periods we adjusted the expected frequencies according to the number of observation days in each period.

Interaction data

For each dyad of two known males we calculated: (i) the number of agonistic interactions won and lost by each animal (dominance situations); (ii) the number of situations where a male arrived and took over the tending position from another male (takeover situations); (iii) the number of situations where the tending male left apparently unforced and another usually coursing male started to tend the female (inheritance situations); and (iv) the number of situations where one male adopted the coursing tactic next to the other, tending male (tend-course situations). To avoid pseudo-replication we always considered only the first situation observed for each male-dyad per female and day. In order to obtain information on the temporal consistency of dominance, takeover, inheritance and tend-course relationships between two specific males during the rut, we evaluated the proportion of dyads which were won always by the same of the two males.

Finally, to test whether (i) takeovers took place without preceding horn fights between two males and (ii) whether the overall winner (male with more encounters won) 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 we conducted binomial-tests (Sheskin 2004).

Results

Courtship behaviour

The proportion of active time allocated to courtship behaviours by males changed significantly between the observation periods (Mixed Model ANOVA; period: $F_{5,148} = 15.38$, $p < 0.001$; year: $F_{2,148} = 3.44$, $p = 0.035$; Animal ID: $F_{69,148} = 0.76$, $p = 0.90$). A marked increase of about 10% was detected between the two periods preceding the rut. Maximal pre-rut level remained however lower than the peak (24.2%) during the first two weeks of rut. During the following weeks, courtship behaviour successively dropped back to pre-rut levels (Fig. 1a).

Agonistic behaviour & horn fights

The proportion of time spent in agonistic behaviours by males varied between observation periods (Mixed Model ANOVA; period: $F_{5,148} = 9.25$, $p < 0.001$; year: $F_{2,148} = 0.13$, $p = 0.87$; Animal ID: $F_{69,148} = 0.67$, $p = 0.97$). During the two pre-rut periods males allocated on average about 5.5 and 7.9% of their active time to this behavioural category. After the beginning of the rut, time spent in agonistic behaviours decreased significantly to about 1.1% and remained nearly unchanged during the two following periods. Agonistic behaviour significantly increased again to about 5.0% during the last observation period (Fig. 1b).

In total 86 horn fights between males were recorded during the three years of the study. Chi-square goodness-of-fit tests showed that these fights were not equally distributed across periods (d.f. = 1, $\chi^2 = 9.47$, $p < 0.001$). Thus, more fights than expected by chance were observed during the pre-rut period, and less fights during the rut (Table 1).

Horn fights and takeovers

In none of the observed 176 takeovers (72, 58 and 46 in the three years, respectively) males were involved in horn fights (Binomial test for dyads: 05/06: N = 35, exceptions = 0, $p < 0.0001$; 06/07: N = 54, exceptions = 0, $p < 0.0001$, 07/08: N=33, exceptions = 0, $p < 0.0001$), meaning that all observed takeovers happened without any foregoing horn fights among males in all three years.

Consistency of relationships during the rut

Irrespective of the investigated category of dyadic relationships (i.e dominance, takeover, inheritance or tend-course situation) a high consistency (of > 90%) between the outcomes of repeated encounters existed during all three rutting periods (Table 2).

Having a closer look on the few exceptions of the dominance situations, it turned out that in 9 of the 19 involved dyads the concerned males had also been observed engaging in horn fights with each-other during the rut. The number of fights within these dyads was by far higher than expected by chance (Binomial test: expected number of fights: 1.68, observed number of fights: 9, N = 19, $p < 0.0001$). In 8 of 10 of the inconsistent dyads (with ≤2 encounters after the occurrence of the first inconsistency) dominance relationships only changed once, indicating that they usually remained stable after the change happened.

Regarding the outliers in the access-to-female situations, it can, furthermore, be noted that in the case of the only inconsistent takeover situation in 07/08, as well as in two of the three inconsistent tend-course situations in 07/08 male-dyads were involved which also showed inconsistencies in the dominance relationship during the rut mentioned above.

Additional analyses showed that the fraction of dyads exhibiting inconsistencies in the dominance relationships did not statistically differ between the pre-rut periods and the rutting periods in each year (Table 3).

Correspondence of dominance relationships and access-to-females relationships

In 89.2-100% of the dyads, depending on the investigated category (i.e. takeover, inheritance, tend-course situation) and the year of observation, the winner determined by interaction encounters coincided with the winner determined by the access-to-female situations (Table 4). Hence, ordinarily the dominant of two males gained (takeover situation) and hold (tend-course situation) unrestricted access to a specific female while the subordinate one 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 (until then coursing) male obtained unrestricted access to the female (inheritance situation; Table 4).
In all of the six dyads where the dominance relationships did not correspond with the outcome of the access-to-female situations and for which we have the necessary data, inconsistencies in the dominance relationship were detected.

Temporal occurrence of agonistic behaviour in other ungulates

The review of quantitative studies on the timing of agonistic behaviour in relation to the mating activity revealed that in 10 out of 12 polygynous ungulates (including this study on Alpine ibex), some or all recorded forms of agonistic behaviours peaked during the principal rutting season (Table 5). The only two exceptions with this regard were Alpine ibex (this study) and Spanish ibex, *Capra pyrenaica*. In 3 different cervid species (i.e. fallow deer, *Dama dama,* mule deer, *Odocoileus hemionus* and white-tailed deer, *Odocoileus viriginianus*), some forms of agonistic behaviours were found to culminate before the rutting season in a number of populations. Apart from Alpine ibex (this study), fighting, the most pronounced form of an agonistic interaction, was only in 2 populations of white-tailed deer observed to peak clearly during the pre-rut season. In 1 population of mule deer ʿritualized fights' were more common during the pre-rut period, whereas, so called 'serious fights' were reportedly more frequent during the rut (Kucera 1978). In the 5 remaining species in which fighting was recorded it was most frequent during the rutting season (Table 5).

Discussion

In support of our hypothesis the results showed that male Alpine ibex markedly reduced intra-male competitions during the rut. They substantially cut down on the time they allocated to agonistic behaviours and decreased the number of horn fights during the mating season compared with before. Observations in the same population suggest that this pattern cannot be the result of a low level of intra-male competition, since single receptive females were associated by on average 4, up to 11 males trying to gain mating access to receptive females (Willisch & Neuhaus in press). 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 highest (Hsu et al. 2005; Parker 1974). However, in 10 of 12 polygynous species (including the Alpine ibex), for which the necessary data is available, some or all agonistic behaviours culminated concomitantly with mating activities, suggesting that intra-male interactions are usually more frequent when males compete for females in oestrous. Likewise, our review shows that in most species agonistic encounters among males are more likely to escalate, and thus to end in fights, during peak mating season. The only exceptions concerning fights were the two cervid species mule deer and white-tailed deer, in which fighting appeared to be more frequent during the pre-rut season. However, in these two species other agonistic behaviours were observed to culminate during the peak of mating activity (Hirth 1977; Kucera 1978).

The question arises, how males of the highly polygynous 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 atypical behavioural pattern is the establishment of stable and strictly binding dominance relationships among individual males which render unnecessary to fight for access over disputed resources such as mating partners. Accordingly, we could demonstrate that during the rut very stable dominance relationships between male Alpine ibex existed determining which one of the two males in a dyad would gain, inherit or hold access to females. In addition, we also showed that physical aggression in the form of horn 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 horn fights were much more frequent than expected by chance among male dyads presenting inconsistencies in their dominance relationships. The observation that in 8 of 10 inconsistent dyads the dominance relationships only changed once, moreover, suggests that the relationships normally remained consistent after a shift had happened.

The establishment of stable dominance relationships seems to be wide-spread among socially living animals, including males of some ungulates (e.g., fallow deer: Jennings et al. 2006; McElligott et al. 1998; bighorn sheep, *Ovis canadensis*: Pelletier and Festa-Bianchet 2006; red deer: Appleby 1982). Still, among these species, intense agonistic interactions for access to receptive females appear often to persist at high levels during the rut and are thus not reduced. In red deer and fallow deer, for instance, 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); and this despite the existence of 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 (Hsu et al. 2005; Parker 1974), contrasts sharply with the conservative behaviour exhibited by male Alpine ibex during the rut. Thus, subordinate male Alpine ibex behaved overall extremely reluctant towards their dominant competitors. Overt aggression was never used by them as a means to achieve access to receptive females (as is often the case in polygynous species), and they usually evaded dominant males when being approached by them. As a consequence, subordinates either left receptive females tended by dominant males, or they adopted the coursing tactic (Willisch & Neuhaus in press). 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 being too close to the defended females. Finally, it has never been observed that subordinate male Alpine ibex disturbed mating attempts by dominant males, as it may occur 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 at first glance be not very evident, 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 (Hsu et al. 2005; Parker 1974). Life-history theory, however, suggests that associated costs in doing so might simply be too high compared to the likely minor benefits in form of few achieved paternities. 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). Because in Alpine ibex males have to attain a relatively high age of about 9 years before becoming competitive enough to tend receptive females (as suggested by Willisch Neuhaus in press), they even have to be more cautious each year to attain that critical age than species whose reproductive peak is earlier in life (such as, for instance, red deer, Clutton-Brock et al. 1982, or Soay sheep, Clutton-Brock and Pemberton 2004). This is because the overall chances to survive a certain number of years is declining exponentially with the number of years to survive. Overt and costly mating behaviour may, furthermore, not only contribute to elevated mortality risks, but also 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 adult body sizes below average, resulting ultimately in inferior reproductive potential and success (Clutton-Brock and Pemberton 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, 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). In this respect, our results indicate that the reluctant mating behaviour of young coursing male Alpine ibex targets primarily good survival perspectives and high growth rates, whereas the siring of offspring seems to be only of secondary importance.

Cost-benefit trade-offs are likely to be further modulated by external factors, such as animal density, predator pressure, climate and topography (e.g., Clutton-Brock and Pemberton 2004; Mysterud et al. 2005; Yoccoz et al. 2002). In the case of male Alpine ibex, this means that their risks and costs associated with physical interactions during the rut (such as energetic depletion and exhaustion, or injuries and death) might even be accentuated compared to other species by the fact that mating usually is taking place under extreme climatic conditions in winter and in very exposed areas. Hence, attacking or fighting in steep slopes or vertical cliffs can easily end in serious injuries or death due to fall (C.S. Willisch, pers. observation); and recovering from long and exhausting fights may be more difficult when vegetation is largely covered by snow and the nutritional content is poor. On the other hand, perspectives to survive to the age when reaching full adult body size and, hence the physical potential to monopolize multiple receptive females during the rut might be generally higher in male Alpine ibex than in other species which are, for instance, subject to heavier predation, or which are living in less constant environments (Clutton-Brock and Pemberton 2004).

Whatever the ultimate reasons are, 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 by our review on the temporal occurrence of the agonistic behaviours, these activities typically peak at that time of the year when females are receptive and males invest already much of their time and energy to courtship and mating behaviours. Together with severe reductions in restoring activities (such as feeding and / or lying, see e.g., Miquelle 1990; Pelletier 2005; Willisch and Ingold 2007), the high energy expenditures due to agonistic interactions lead inevitably to strongly negative energy budgets (Pelletier 2005; but see McElligott et al. 2003), which, in turn, contribute to drastic losses in body weight and fat reserves of males (Bobek et al. 1990; Forsyth et al. 2005; McElligott et al. 2003; Mysterud et al. 2004; Mysterud et al. 2005; Yoccoz et al. 2002) and finally to elevated mortality risks. Because male Alpine ibex allocate only very little time to agonistic behaviours during the rut, a significant component of their energetic expenditures will be substantially reduced in contrast to other species.

Overall, this study provides clear support for the hypothesis that male Alpine ibex are able to reduce energetically costly intra-male interaction during the rut by the adherence to pre-established dominance relationships among them. Since the rut-related losses of energy are likely to affect the subsequent survival of males negatively, this study indicates that the specific social system of male Alpine ibex may contribute to the extraordinary low mortality rates of adult males reported for this species (Toïgo et al. 2007). Consequently, our study shows that the social system can have important implications for the energetics and survival of animals, and thus constitutes an important part of their life-history strategy.

Acknowledgements

We thank P. Decristophoris, I. Glanzmann, N. Grandjean, B. Nussberger and C. Wittker for their assistance in data collection. Furthermore we appreciate the help of numerous people in capturing and marking Alpine ibex, above all J.-C. Roch, M.-P. Ryser-Degiorgis and N. Marreros, as well as K. Bieri, P. Deleury, C. Hebeisen, B. Hofer, I. Leathwood, H. Nimmervoll. We are particularly grateful to S. Sachot and J.-C. Roch of the Canton Vaud who permitted and supported the conduction of this study in the population of ‘Cape au Moine’ (VD). Financial support was provided by the Federal Office of the Environment (FOEN).

References

Abderhalden, W. 2005. Raumnutzung und sexuelle Segregation beim Alpensteinbock *Capra ibex ibex*, Nationalpark-Forschung Schweiz 92.

Aeschbacher, A. 1978. Das Brunftverhalten des Alpensteinbocks. Eugen Rentsch Verlag, Erlenbach-Zürich.

Alados, C. L. 1986. Aggressive behavior, sexual strategies and their relation to age in male Spanish ibex (*Capra pyrenaica*), Behavioural Processes 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 holdingi fallow deer, Canadian Journal of Zoology - Revue Canadienne de Zoologie 71:376-383.

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

Appleby, M. C. 1982. The consequences and causes of high social rank in red deer stags, Behaviour 80:259-273.

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

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

Buschhaus, N. L., K. E. Lagory, and D. H. Taylor. 1990. Behavior in an introduced population of fallow deer during the rut, American Midland Naturalist 124**:**318-329.

Clutton-Brock, T. H., and S. D. Albon. 1979. Roaring of red deer and the evolution of honest advertisement, Behaviour 69**:**145-170.

Clutton-Brock, T. H., S. D. Albon, R. M. Gibson, and F. E. Guinness. 1979. Logical stag - adaptive aspects of fighting in red deer (*Cervus elaphus* L), Animal Behaviour 27**:**211-225.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer. Behavior and ecology of two sexes. The University of Chicago Press, Chicago.

Clutton-Brock, T. H., and J. Pemberton. 2004. Soay sheep. Dynamics and selection in an island population. Cambridge University Press, Cambridge.

Cluttonbrock, T. H., D. Green, M. Hiraiwa-Hasegawa, and S. D. Albon. 1988. Passing the buck: resource defence, lek breeding and mate choice in fallow deer, Behavioral Ecology and Sociobiology 23**:**281-296.

Conradt, L., and T. J. Roper. 2000. Activity synchrony and social cohesion: a fission-fusion model, Proceedings of the Royal Society of London Series B-Biological Sciences 267**:**2213-2218.

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

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

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.

Fryxell, J. M. 1987. Lek breeding and territorial aggression in white-eared kob, Ethology 75**:**211-220.

Georgii, B., and W. Schroder. 1983. Home range and activity patterns of male red deer (*Cervus elaphus* L) in the alps, Oecologia 58**:**238-248.

Grignolio, S., F. Parrini, B. Bassano, S. Luccarini, and M. Apollonio. 2003. Habitat selection in adult males of Alpine ibex, Capra ibex ibex, Folia Zoologica 52**:**113-120.

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

Hirth, D. H. 1977. Social behavior of white-tailed deer in relation to habitat, Wildlife Monographs 53:3-55.

Hoem, S. A., C. Melis, J. D. C. Linnell, and R. Andersen. 2007. Fighting behaviour in territorial male roe deer Capreolus capreolus: the effects of antler size and residence, European Journal of Wildlife Research 53:1-8.

Hogg, J. T. 1987. Intrasexual competition and mate choice in Rocky Mountain bighorn sheep, Ethology 75:119-144.

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.

Hsu, Y., R. L. Earley, and L. L. Wolf. 2005. Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes, Biological Reviews 80:1-42.

Ingold, P., U. Pfister, E. Baechler, and P. Enggist-Dueblin. 1998. Pattern and rhythm of activity in alpine chamois (*Rupicapra r. rupicapra*) during winter, Zeitschrift für Säugetierkunde - International Journal of Mammalian Biology 63:183-185.

Jennings, D. J., M. P. Gammell, C. M. Carlin, and T. J. Hayden. 2003. Is the parallel walk between competing male fallow deer, *Dama dama*, a lateral display of individual quality? Animal Behaviour 65:1005-1012.

Jennings, D. J., M. P. Gammell, C. M. Carlin, and T. J. Hayden. 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, P. E., F. Messier, and C. C. Gates. 1992. Search or relax – the case of bachelor wood bison, Behavioral Ecology and Sociobiology 31:195-203.

Komers, P. E., F. Messier, and C. C. Gates. 1994a. Plasticity of reproductive behavior in wood bison bulls - on risks and opportunities, Ethology Ecology & Evolution 6:481-495.

Komers, P. E., F. Messier, and C. C. Gates. 1994b. Plasticity of reproductive behavior in wood bison bulls - when subadults are given a chance, Ethology Ecology & Evolution 6:313-330.

Koutnik, D. L. 1981. Sex related differences in the seasonality of agonistic behavior in mule deer, Journal of Mammalogy 62:1-11.

Kucera, T. E. 1978. Social behavior and breeding system of desert mule deer, Journal of Mammalogy 59:463-476.

Lott, D. F. 1981. Sexual behavior and intersexual strategies in American bison, Zeitschrift für Tierpsychologie - Journal of Comparative Ethology 56:97-114.

Maher, C. R. 1991. Activity budgets and mating system of male pronghorn antelope at Sheldon National wildlife refuge, Nevada, Journal of Mammalogy 72:739-744.

Maher, C. R. 1994. Pronghorn male spatial organization - Population differences in degree of non-territoriality, Canadian Journal of Zoology - Revue Canadienne de Zoologie 72:455-464.

Mainguy, J., S. D. Cote, E. Cardinal, and M. Houle. 2008. Mating tactics and mate choice in relation to age and social rank in male mountain goats, Journal of Mammalogy 89:626-635.

McElligott, A. G., R. Altwegg, and T. J. Hayden. 2002. Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*), Proceedings Of The Royal Society Of London Series B-Biological Sciences 269:1129-1137.

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.

McElligott, A. G., K. P. O'neill, and T. J. Hayden. 1999. Cumulative long-term investment in vocalization and mating success of fallow bucks, *Dama dama*, Animal Behaviour 57:1159-1167.

Melis, C., S. A. Hoem, J. D. C. Linnell, and R. Andersen. 2005. Age-specific reproductive behaviours in male roe deer *Capreolus capreolus*, Acta Theriologica 50:445-452.

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

Miura, S. 1984. Social behavior and territoriality in male sika deer (*Cervus nippon* Temminck 1838) during the rut, Zeitschrift für Tierpsychologie - Journal pf Comparative Ethology 64:33-73.

Moore, N. P., P. F. Kelly, J. P. Cahill, and T. J. Hayden. 1995. Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population, Behavioral Ecology and Sociobiology 36:91-100.

Mysterud, A., R. Langvatn, and N. C. Stenseth. 2004. Patterns of reproductive effort in male ungulates, Journal of Zoology 264:209-215.

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.

Nefdt, R. J. C. 1995. Disruptions of matings, harassment and lek-breeding in kafue lechwe antelope, Animal Behaviour 49:419-429.

Nefdt, R. J. C., and S. J. Thirgood. 1997. Lekking, resource defense, and harassment in two subspecies of lechwe antelope, Behavioral Ecology 8:1-9.

Olsson, M. 1993. Contest success and mate guarding in male sand lizards, *Lacerta agilis*, Animal Behaviour 46:408-409.

Parker, G. A. 1974. Assessment strategy and evolution of fighting behavior, Journal of Theoretical Biology 47:223-243.

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

Pelabon, C., P. E. Komers, B. Birgersson, and K. Ekvall. 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, 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.

Pelletier, F., J. T. Hogg, and M. Festa-Bianchet. 2006. Male mating effort in a polygynous ungulate, Behavioral Ecology and Sociobiology 60:645-654.

Pianka, E. R., and W. S. Parker. 1975. Age-Specific Reproductive Tactics, American Naturalist 109:453-464.

Preston, B. T., I. R. Stevenson, J. M. Pemberton, and K. Wilson. 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.

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.

Sheskin, D. J. 2004. Handbook of parametric and nonparametric statistical procedures, Third ed. Chapman & Hall/CRC, Boca Raton.

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 Series B-Biological Sciences 262:267-275.

Taillon, J., and S. D. Cote. 2006. The role of previous social encounters and body mass in determining social rank: an experiment with white-tailed deer, Animal Behaviour 72:1103-1110.

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

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

Van Soest, P. J. 1994. Nutrional ecology of the ruminant., 2nd ed. Cornell University Press, Ithaca.

Villaret, J. C., and R. Bon. 1998. Sociality and relationships in Alpine ibex (*Capra ibex*), Revue d'ecologie - La terre et la vie 53**:**153-170.

Wells, M. S. 1988. Effects of body size and resource value on fighting behavior in a jumping spider, Animal Behaviour 36**:**321-326.

Willisch, C. S., and P. Ingold. 2007. Feeding or resting? The strategy of rutting male Alpine chamois, Ethology 113**:**97-104.

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

Yoccoz, N. G., A. Mysterud, R. Langvatn, and N. C. Stenseth. 2002. Age- and density-dependent reproductive effort in male red deer, Proceedings of the Royal Society of London Series B-Biological Sciences 269**:**1523-1528.

Figures

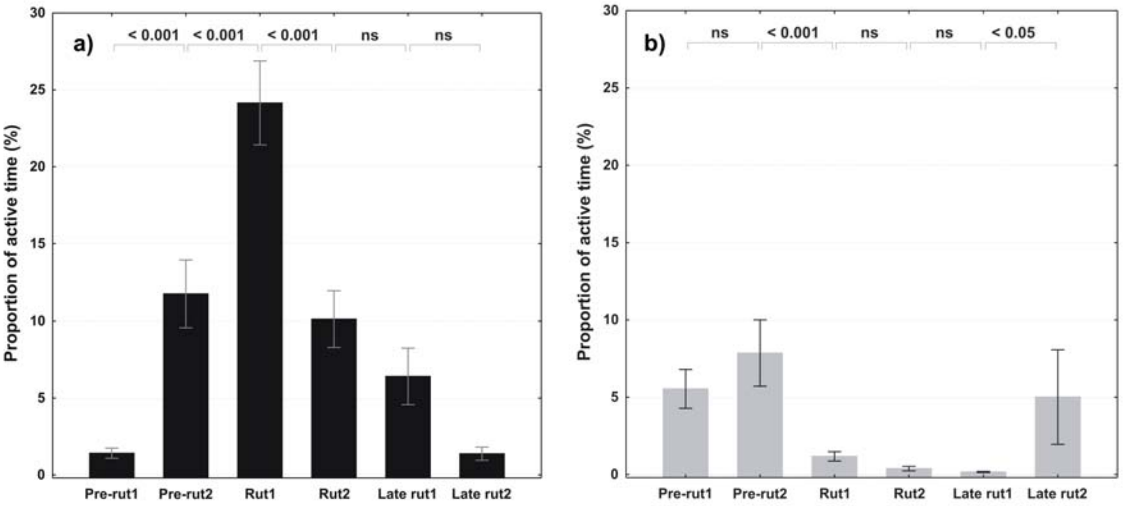

Fig. 1: Mean (±SE) proportion of active time spent in courtship (a) and agonistic behaviours (b) by male Alpine ibex during different periods. Significance levels between consecutive periods using Fisher's LSD test are displayed at the top of the graphs (ns: non-significant differences at p-level of 0.05).

Tables

Table 1: Observed versus expected (adjusted for the number of observation days) number of horn fights during the pre-rut and the rut, and the corresponding statistics for the chi-square goodness-of-fit test (OD: number of observation days per period; OF: number of observed fights; EF: number of expected fights).

	OD	**OF**	**EF**	**$(OF-EF)^2$ / EF**
Pre-rut	54	44	30.44	6.04
Rut	95	40	53.56	3.43
				$\chi^2 = 9.47$

Table 2: Consistency of winner-loser relationships in male dyads with at least two encounters in dominance, takeover, inheritance and tend-course situations for the different rutting periods 2005/06, 2006/07 and 2007/08, respectively.

	Dominance			**Takeover**			**Inheritance**			**Tend-course**		
	2005/06	**2006/07**	**2007/08**	**2005/06**	**2006/07**	**2007/08**	**2005/06**	**2006/07**	**2007/08**	**2005/06**	**2006/07**	**2007/08**
Number of dyads with at least 2 encounters	60	47	112	11	3	10	3	2	3	43	70	62
Number of these dyads always won by the same male	54 (90%)	44 (93.6%)	102 (91.1%)	11 (100%)	3 (100%)	9 (90%)	3 (100%)	2 (100%)	3 (100%)	43 (100%)	70 (100%)	60 (96.7%)

Table 3: Number of observed male dyads exhibiting inconsistencies in their dominance relationships (meaning that dominance encounters are not always won by the same male of the dyad) in the various pre-rut periods compared to the corresponding numbers in the subsequent rutting periods.

	2005/06		**2006/07**		**2007/08**	
	Pre-rut	**Rut**	**Pre-rut**	**Rut**	**Pre-rut**	**Rut**
Number of dyads with at least 2 encounters	26	60	44	47	36	112
Number of these dyads with inconsistencies	0 (0%)	6 (10%)	5 (11.4%)	3 (6.3%)	4 (11.1%)	10 (8.9%)
Expected number of inconsistent dyads	1.81	4.18	3.87	4.13	3.41	10.60
Chi-square goodness-of-fit tests	$\chi^2 = 2.60$	$p = 0.26$	$\chi^2 = 0.64$	$p = 0.80$	$\chi^2 = 0.14$	$p = 0.96$

Table 4: 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 2005/06, 2006/07 and 2007/08, respectively.

	Takeover			**Inheritance**			**Tend-course**		
	2005/06	**2006/07**	**2007/08**	**2005/06**	**2006/07**	**2007/08**	**2005/06**	**2006/07**	**2007/08**
Number of dyads of which the dominance relationship is known	21	29	28	14	7	10	57	71	102
Number of dyads where winner by dominance is winner by access-to-female relationship	19 (90.5%)	27 (93.1%)	25 (89.2%)	14 (100%)	7 (100%)	10 (100%)	55 (96.5%)	71 (100%)	99 (97.1%)
Binomial test p (two-tailed)	0.0002	< 0.0001	0.00003	0.0001	0.0156	0.0020	< 0.0001	< 0.0001	< 0.0001

Table 5: Number of populations in which agonistic behaviors culminate before or concomitantly with the peak of mating activity. Behavioral categories: AG: agonistic behaviour in general; DI: displays; DP: displacements; FT: fights; VO: vocalizations.

Taxa	**Before mating peak**	**During mating peak**	**References**
Bovidae:			
Bison bison		2 (AG, DP, FT)	Komers et al. (1992); Komers et al. (1994a); Komers et al. (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); Maher (1994)
Capreolus capreolus		1 (AG)	Melis et al. (2005)
Cervus elaphus		1 (DP, FT, VO)	Clutton-Brock and Albon (1979); Clutton-Brock et al. (1979); Clutton-Brock et al. (1982)
Cervus Nippon		1 (AG)	Miura (1984); Buschhaus et al. (1990)
Dama dama	1 (DP)	3 (AG, DP, FT, VO)	Cluttonbrock et al. (1988); Buschhaus et al. (1990); McElligott et al. (1998); McElligott et al. (1999); Pelabon et al. (1999)
Odocoileus hemionus	2 (AG, rFT[1])	1 (AG, sFT[1])	Kucera (1978); Koutnik (1981)
Odocoileus viriginianus	2 (FT)	1 (AG)	Hirth (1977)

1) 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.

CHAPTER 3

LIFE-HISTORY STRATEGY IN LONG-LIVED MALE ALPINE IBEX (*CAPRA IBEX*) AND THE SIGNIFICANCE OF EARLY REPRODUCTION VIA SNEAKING TACTICS

Christian S. Willisch, Iris Biebach, Ursina Koller, Thomas Bucher, Nelson Marreros, Marie-Pierre Ryser-Degiorgis, Lukas Keller, Peter Neuhaus

Corresponding author:
Christian S. Willisch
Department of Eco-Ethology, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2009 Neuchâtel, Switzerland
Email: willichristian@yahoo.com

Running title:
Reproduction in long-lived male Alpine ibex

Print title:
LIFE-HISTORY STRATEGY IN LONG-LIVED MALE ALPINE IBEX (*CAPRA IBEX*) AND THE SIGNIFICANCE OF EARLY REPRODUCTION VIA SNEAKING TACTICS

Authors:
Christian S. Willisch1), Iris Biebach3), Ursina Koller3), Thomas Bucher3), Nelson Marreros4), Marie-Pierre Ryser-Degiorgis4), Lukas Keller3), Peter Neuhaus1,2)

Addresses:
1) Department of Eco-Ethology, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2009 Neuchâtel, Switzerland
2) Department of Biological Sciences, University of Calgary, 2500 University Dr. NW, Calgary AB, T2N 1N4, Canada
3) Zoological Museum, University of Zurich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland
4) Centre for Fish and Wildlife Health, Vetsuisse Faculty, University of Bern, Länggass-Strasse 122, CH-3001 Bern, Switzerland

Abstract

Life-history theory suggests that young animals adjust their investments into current reproduction each year depending on their survival perspectives. We therefore assumed that reproduction in male ungulates via sneaking tactics at young age should become less important with improving survival perspectives of animals. We tested this hypothesis in Alpine ibex, a long-lived mountain ungulate, in which males adopt two alternative mating tactics during the rut and exhibit an outstandingly high adult survival. Paternity was inferred in two offspring cohorts in a population in the Swiss Alps by the use of molecular and behavioural data within a Bayesian framework. We parameterized 4 models to estimate the effects of age, dominance and mating tactic on the likelihood of paternity. In accordance with our hypothesis, reproductive success was heavily skewed towards older, dominant males that typically monopolized access to receptive females by the adoption of the ‘tending’ tactic, while success among young, subordinate males via the sneaking tactic ‘coursing’ was overall low and rare. Compared with other ungulate species with higher mortality rates reproduction among young male Alpine ibex was, as predicted, overall much lower and more sporadic. Finally, a relatively high reproductive skew emerged, denoting a big potential for selection in male Alpine ibex. This study supports the theory that survival prospects of males modulate the investments into reproduction via alternative mating tactics early in life. Our results indicate that the life-history strategy of male Alpine ibex targets for long life, slow and prolonged growth and late reproduction.

Introduction

Energy is a limited resource that has set important constraints under which life has evolved. Hence, all organisms have to adopt strategies to acquire, store and allocate the energy disposable to them (Kozlowski 1992). Iteroparous animals are faced during each breeding season with the trade-off of how much energy they should invest into current and how much into future reproduction (Stearns 1976; Williams 1966). Investments into reproduction are costly and therefore reduce future reproductive success (Bell 1980; Stevenson and Bancroft 1995). The residual reproductive value of individuals will consequently decline once they have started to breed (Clutton-Brock 1984; Pianka and Parker 1975). In animals, in which size is an important determinant of reproductive success, individuals should therefore be assumed to first direct their investments into growth and survival before starting with reproduction (Stearns 1992). Accordingly, meta-analyses of life history traits in a variety of animal species revealed that, while accounting for differences in body size and phylogeny, growth and survival both co-varied with reproduction. Long life related to slow growth, delayed age of maturity and start of reproduction, and low rates of reproduction, whereas short life was found to be associated with fast growth, early maturity and start of reproduction, as well as high rates of reproduction, a pattern often referred to as the ‘slow-fast continuum’ (e.g., Dobson and Oli 2007; Harvey and Zammuto 1985; Promislow and Harvey 1990).

In animals in which access to potential mating partners is strongly size-dependent it might accordingly be expected that individuals should wait with reproduction until they are full-grown (Stearns 1992). One group in which such a pattern could be wide-spread are males of polygynous ungulates whose potential to monopolize access to receptive females has been shown to be restricted to mainly older individuals (e.g., Clutton-Brock et al. 1982; Komers et al. 1992; Mainguy et al. 2008; McElligott and Hayden 2000; Pelletier et al. 2006; Willisch and Neuhaus in press; Wolff 1998). Contrary to this prediction, however, molecular analyses unequivocally revealed that also younger, not full-grown male ungulates can be quite successful in siring offspring (bighorn sheep, *Ovis canadensis*: Coltman et al. 2002; Soay sheep, *Ovis aries*: Coltman et al. 1999a; Coltman et al. 1999b; Pemberton et al. 1999; Preston et al. 2001; reindeer, *Rangifer tarandus*: Roed et al. 2005; white-tailed deer, *Odocoileus virginianus*: Sorin 2004).

As in other taxa (Oliveira et al. 2008), also in ungulates, paternities achieved by young and, hence, small animals are likely to be mainly the outcome of ‘sneaky’ mating tactics where animals try to steal copulations from big-sized, access-defending males (Hogg and Forbes 1997; Stevenson et al. 2004; Taborsky 1997; Willisch and Neuhaus in press). Sneaking tactics are likely to evolve, when portions of sexually mature males are excluded from reproduction by a restricted number of superior individuals in the population (Emlen and Oring 1977; Shuster and Wade 2003). Contrary to expectations that these tactics generally incur only little costs (Taborsky et al. 2008), various observations indicate that the use of them in male ungulates may be energetically costly (Pelletier 2005; Yoccoz et al. 2002; but see Willisch and Neuhaus in press) and dangerous (Hogg and Forbes 1997; Preston et al. 2001; Saunders et al. 2005), with supposedly non-trivial negative effects on future reproductive success (Stevenson and Bancroft 1995; Stevenson et al. 2004). Because of this important trade-off, a young male’s investment into sneaking tactics should negatively correlate with his probability to survive to the age when he is big and competitive enough to successfully adopt a tactic to monopolize access to receptive females. Accordingly, in male ungulates with high survival, we should expect reproductive success to be comparatively heavily biased towards older, access-defending males, while at the same time success among younger, sneaking males should be relatively small.

We tested this idea in Alpine ibex, *Capra ibex*, where males aged 2-8 years were reported to exhibit an exceptional annual survival of >98%, largely irrespective of the ecological conditions (Toïgo et al. 2007). Male Alpine ibex adopt two alternative mating tactics during the rut (Willisch and Neuhaus in press): a primary tactic, termed ‘tending’ which is mainly used by older males in the population to monopolize access to receptive females, and a sneaking tactic termed ‘coursing’ which is typically adopted by younger males to obtain transient mating opportunities to tended females. In accordance with the life-history considerations outlined above, time budget analyses during the rut already indicated that young males invest only little energy into reproduction compared to older ones. Hence, it was shown that males while coursing allocated overall a relatively low proportion of their time to moving, courtship and agonistic behaviours, whereas much time was used for feeding, lying and standing (Willisch and Neuhaus in press). Behavioural evidence, furthermore, suggested that coursing is the less promising tactic of the two with regard to the number of observed copulations (Willisch and Neuhaus in press). However, because molecular data on reproduction in male Alpine ibex were still missing, it was not yet clear whether reproductive success in male Alpine ibex would indeed be heavily skewed towards older individuals in population, as predicted by our hypothesis, while younger ones would only succeed in a minor reproductive success. To test this, we collected DNA samples of two offspring cohorts, their mothers and potential fathers in a population of Alpine ibex in the Swiss Alps and performed paternity analyses within a Bayesian framework. Behavioural observations during the two preceding rutting seasons were conducted to obtain data on individual male social and mating behaviour. Supposed positive effects of high age on reproductive success in males were likely to be mediated through high dominance and the adoption of the tending tactic during the rut (see Willisch and Neuhaus in press, submitted). We therefore expected these variables to have a strong positive effect on the likelihood of paternity. Finally, we compared the results of this study with data on males of other polygynous ungulates with differing mortality rates, because reproductive skew towards older males should be more pronounced in species with higher survival rates.

Methods

Study animals

The study was carried out in the ‘Cape au Moine’ population of Alpine ibex north of the village of Les Diablerets (VD) in the Swiss Alps; for a detailed description see Willisch and Neuhaus (in press). In brief, the population consisted of up to 270 animals (Table 1) and with some harvest taking place every year. Alpine ibex are sexually highly dimorphic mountain ungulates, with adult males being on average more than twice as heavy (95 kg versus 45 kg; Loison et al. 1999) and possessing much larger horns than adult females (>90 cm versus >30 cm; Lüps et al. 2007). Adult males between 2 and 8 years exhibit extremely high yearly survival rates of > 98% irrespective of ecological conditions (Toïgo et al. 2007); their body size does normally not become asymptotic until the age of 8 years (Lüps et al. 2007).

Whereas females with their young stayed in the study area year-round, part of the males were known to show seasonal migration between this and two adjacent populations.

Data collection

Data collection comprised three different parts: First, the collection of DNA samples of kids born in 2006 and 2007, and samples of their mothers and potential fathers; second, behavioural observations and censuses during the two preceding pre-rut and rutting seasons in 2005-06 and 2006-07; and third, censuses during fall / winter in 2006-07 and 2007-08 when kids were about 5-8 months old. In the first year of the study, observations before and during the rutting season, as well as the collection of the DNA samples of the kids and their mothers were restricted to only a part of the study area not covering the whole population.

Individual recognition and age determination

At the time of the study, in total 68 males (> 2 years old) and 18 females (> 2 years old) in the study population could be individually recognized based on unique characteristics of their horns and coat coloration. Another 30 animals (20 males, and 10 females) were individually marked using colored and numbered ear tags (for details see Willisch and Neuhaus in press).

The age of male Alpine ibex was determined by counting the conspicuous annuli on the outer side of the horns (Ratti and Habermehl 1977). In animals that were captured, found dead or were shot this was done at close distance. For the remaining males used in this study, age determination was performed retrospectively by inspecting all the available photographs taken from these animals (Willisch and Neuhaus in press).

Behavioural observations during the rut

Between November and December in 2005-06 and 2006-07 behavioural observations on individually marked or recognizable Alpine ibex were carried out to obtain (i) data to establish linear dominance hierarchies among rutting males, as well as (ii) data that allowed us to calculate a tactic index which reflected the extent to which individual males adopted the tending and the coursing tactic.

To establish linear dominance hierarchies (Drews 1993) among males during the rut in 2005-06 and 2006-07 we constructed dyadic winner-loser matrices. Individuals were ranked based on the so called 'I & SI' method in which the number and strength of detected ranking inconsistencies were minimized (De Vries 1998; De Vries and Appleby 2000; De Vries et al. 1993). This approach was considered to be ideal for our purposes, as it did not make any assumptions about the form of the probabilities of winning and losing (De Vries 1998; De Vries and Appleby 2000; Gammell et al. 2003). Only animals which interacted with at least 5 other individuals (2005-06: 23 males; 2006-07: 47 males; H. De Vries, pers. comm.; see also Gammell et al. 2003) were included in the data sets. In a male-male dyad an individual was the designated winner of an agonistic encounter (and its opponent the considered loser) when it displaced or mounted his opponent, or when it was following its opponent after a horn fight had taken place. In addition, we also used information derived from situations in which males were competing for access to single receptive females, as they had previously been shown to reflect reliably the dominance relationships among males (Willisch and Neuhaus submitted). Accordingly, we referred to that individual of a male-male dyad as to be the winner, when (i) it took over the tending-access from his opponent, or (ii) when it was observed to tend while his opponent adopted the coursing tactic. Linearity tests were conducted to verify the existence of linear hierarchies among males using Matman 1.1 (Noldus; De Vries et al. 1993). Following these tests, individuals were reordered to fit a linear hierarchy. The resulting ranks of animals were then transformed to standardized ranks by the algorithm 1-(rank/N_x); where N_x is the number of males in the year x (Coté 2000). Standardized ranks varied between 0 (lowest ranking male) and 1 (highest ranking male).

For both rutting periods individual tactic indices were calculated using the formula $T_i / (T_i + C_i)$, where T_i is the total number of times a specific male i had been observed to adopt the tending tactic, and C_i the total number of times the same male i had been observed to adopt the coursing tactic. The tactic index may range from 0 (male adopted exclusively the coursing tactic) to 1 (male adopted exclusively the tending tactic). Although defended females were scanned multiply during the day to obtain information on the adopted mating tactics by the different males only the first observation per female and day was considered in order to avoid pseudo-replication. This selection procedure was unlikely to bias the estimation of the male tactic indices, since instances in which coursing males were subsequently tending a certain female (or vice versa) were overall extremely rare (i.e. 9 of 550 cases in 2005-06; 16 of 1093 cases in 2006-07).

Census data

Between 2005 and 2007-08 daily animal censuses were carried out between November and January to receive information on the size and the sex-age structure of the population, as well as on the presence of individual males during the rut, and kids having survived to 5-8 months of age. Because the whole study area was too big to be monitored within 1 day population-wide censuses were composed of 2 daily censuses performed on consecutive days with good visibility and safe snow conditions.

Genetic data

In total 748 DNA samples were gathered primarily by non-invasive collecting of fresh faeces (Maudet et al. 2004; Wehausen et al. 2004) deposited by observed free-ranging animals in the field. This method yielded 651 samples. The remaining DNA samples comprised 43 blood and 54 tissue samples. All blood samples originated from animals that were captured. Of the tissue samples 5 were obtained using biopsy darts (Biebach 2009), while the remaining ones stemmed from animals that were either legally killed by hunters or found dead. Tissue samples were stored in 100% Ethanol and blood samples in APS buffer at -20°C. Faecal samples were stored in a freezer at -20°C.

In order to obtain fully functional DNA samples of most of the kids born in the two years, their mothers and a significant portion of the potential fathers, animals in the different parts of the study area had been sampled multiple times. Unless the mothers of kids were individually known, we collected faecal samples of kids and mothers on the same occasions. Females were judged to be the mothers of kids when they were lying in contact, or when kids were allowed to suckle. Whenever possible, digital pictures were taken of the sampled animals which were later on used to confirm their identity and to determine their age (see above).

DNA from blood and tissue samples was extracted using commercial kits as described in Biebach (2009). To extract DNA from faecal samples, the outermost layers of 3 ≥ pellets per sample were scraped off to obtain 180-220 mg of faecal material (Wehausen et al. 2004).

The material was then further processed using commercial kits (Qiagen Stoolkit, Biosprint). DNA samples were genotyped at 32 microsatellite loci (Appendix 1). We used PCR conditions and multiplex reactions as described in Biebach (2009) with the exception of two modifications for the faecal samples. First, we used always 36 amplification cycles. Second, five loci that showed good amplification success in DNA samples of low quality (JMP29, McM73, OarFCB20, SR-CRSP23, TGLA126) were pooled in a new multiplex reaction with an annealing temperature of 57°C. Allele sizes and genotypes were determined using the software GENEMAPPER 3.7 (Applied Biosystems) and LIZ size standard followed by manual proofreading (for details see Biebach 2009). In contrast to blood and tissue samples, all faecal samples were genotyped ≥ 3 times to account for increased genotyping errors which were due to supposed low quality and quantity of the DNA (Taberlet et al. 1999; Wehausen et al. 2004). The software package GIMLET (Valiere 2002) was subsequently used to build consensus genotypes when at least two of the three replicates produced consistent results. Samples that did not generate genotypes were repeated at least once. If replications did not produce positive results, another sample of the same individual, if available, was analyzed. We estimated locus-specific error rates in faecal samples using GIMLET (Appendix 1). Locus-specific error rates in blood and tissue samples were calculated by Biebach (2009) with the software PEDANT (Johnson and Haydon 2007) using a larger data set. We measured DNA quantity in the faecal samples through a quantitative PCR (QPCR) using the TaqMan-method by amplifying part of the c-myc proto-oncogene (Morin et al. 2001). We used primers and a TaqMan-probe that were developed for seven ungulate species (Bucher 2007). DNA concentrations were determined using a standard curve consisting of 11 dilutions (of Alpine ibex DNA from tissue) ranging from 0.005 ng/µl to 10 ng/µl.

Prior to paternity analyses, identity analyses using CERVUS 3.0 (Kalinowski et al. 2007) and photographs taken of the animals were performed to make sure that multiple samples of single individuals were not mistakenly assigned to different individuals. We, furthermore, removed (i) samples that were genotyped at < 18 loci, (ii) samples of kids without successfully genotyped mothers, and (iii) samples of known males that have never been observed during either of the two rutting periods. While the two first steps aimed to improve the genetic data by removing unpromising samples, the third step intended to exclude males from the paternity analyses, which were likely to have rutted and potentially reproduced elsewhere, hence not in the study population.

Paternity and parameter estimation using MasterBayes

Pedigree reconstruction and the estimation of the parameters of interest were performed in a Bayesian framework using the R package MasterBayes (Version 2.4.2; Hadfield et al. 2006). MasterBayes provided in our case significant advantages compared to other approaches and programs used to infer and analyse paternity. First, MasterBayes did not require making judicious pre-selections when differing genotypes of the same individual existed, as it was able to integrate multiple genotypes of single individuals. Second, it could cope with locus-specific error rates, rendering it unnecessary to specify an overall error rate which would not have adequately reflected the information contained in loci of differing quality. Third, there was no need to pre-determine the proportion of the male population for which genotypes could be obtained; a factor known to affect the confidence intervals with which paternities are assigned (see Marshall et al. 1998; Pemberton et al. 1999). Fourth, the joint estimation of paternity and population-level parameters by MasterBayes has been shown to increase the power of paternity assignment, to reduce the bias in parameter estimation, and to evaluate accurately uncertainty in both (Hadfield et al. 2006; Pemberton 2008).

We fitted four different models to estimate the effects of age (model 1 and 2), dominance rank (model 3) and mating tactics (model 4) on the likelihood of paternity in male Alpine ibex (Table 2). Because dominance ranks and tactic indices were not available for all males, we accounted for this in the corresponding models by replacing all missing values by 0 (zero) and fitting secondary binary variables (missing vs. not missing) as interactions with the variable age (J.D. Hadfield, pers. comm.). Markov chains were run for 1.1 million iterations, with a burn-in of 100 000 iterations and a thinning interval of 1000. In the models 3 and 4, priors were set for the number of unknown sires, as well as for the different parameter estimates. The priors for the unknown sires were log-normal distributed and weakly informative, with a mean of log(15) and a sigma of 0.75. For the remaining parameter estimates priors with means of 0 (zero, i.e. no effect) and variances of pi (which is the closest normal-inverse-logit transformation to a uniform prior on the probability scale) for categorical variables and of 0.02 and 1000 for continuous or mixed variables were used (J.D. Hadfield, pers. comm.). The distributions of the parameters of interest were estimated directly from the 1000 MCMC samples from the posterior distribution of the pedigree, and summarised by the median and the range between quantiles 2.5 and 97.5 (referred to as the 95% credible interval or 95% CI).

Variation in male reproductive success and opportunity for selection

Mean individual male reproductive success, and the mean standardized variance in reproductive success I_m (variance / mean^2) as a measure for the variation in reproductive success and the opportunity for selection (Coltman et al. 1999b; Shuster and Wade 2003), were both calculated from the 1000 MCMC samples from the posterior distribution of the pedigree.

Results

Sex-age structure in 2005-06 and 2006-07

Census data revealed that the restricted study area during the first rut in 2005-06 was inhabited by up to 78 animals, with a mean sex ratio of 0.62 males per female (Table 1). During the rut in 2006-07, when the whole study population was monitored, a maximum of 221 animals were observed, with a mean sex ratio of 0.76. The number of observed males per age class varied during both years, and showed a general trend to decline with increasing age (Fig. 1). The oldest males observed were a 12 year old male in 2005-06, and another 13 year old male in 2006-07. In the two fall-winter censuses following the observed ruts, a maximum of 19 (restricted area) and 63 kids were detected to have survived to the age of 5-8 months in the corresponding areas (Table 1).

Dominance and mating tactics

During both rutting periods linear dominance hierarchies among male Alpine ibex became apparent (2005-06: 146 of 253 possible dyads observed, $h'=0.49$, $p < 0.0001$; 2006-07: 275 of possible 1081 dyads observed, $h' = 0.15$, $p = 0.0002$). Individual dominance ranks of animals were strongly age-dependent (REML for linear age effect: d.f. = 61, $t = 9.93$, $p < 0.0001$, effect size of age: 0.11 ± 0.01; mean ± SE), with males aged 10-11 years being the most dominant individuals, and the youngest males being the most subordinate ones (Fig. 2). Individual tactic indices were also positively age-dependent (REML for linear age effect: d.f. = 54, $t = 8.85$, $p < 0.0001$; effect size of age: 0.20 ± 0.02; mean ± SE). Accordingly, older males of > 6-7 years of age predominately adopted the tending tactic to attain access to receptive females, while younger males of ≤ 5 year of age mainly used the coursing tactic (Fig. 2). As a consequence, strong positive correlations between dominance ranks and tactic indices existed in both years (2005-06: n = 21, r = 0.79, p < 0.0001; 2006-07: n = 36, r = 0.89, p < 0.0001). Tending was the most used tactic by males with a dominance rank of > 0.6, whereas males with lower dominance ranks adopted primarily the coursing tactic.

Number of individual / samples typed

In total, 449 DNA samples (369 faecal samples, 42 blood samples and 38 tissue samples; 217 samples of males, 103 of females, and 129 of juveniles) were successfully genotyped at an average of 23.3 ± 7.5 (mean ± SD) loci. The mean number of alleles detected per locus in these samples was 2.88 ± 1.07 (Appendix 1). Locus-specific rates for allelic dropouts and false alleles based on faecal sample replicates varied around 5.1 ± 6.9 % and 1.6 ± 1.5 %, respectively; whereas the corresponding values for blood and tissue samples estimated by Biebach (2009) varied around 1.1 ± 2.2 % and 0 ± 0.1 %, respectively (Appendix 1). Quantitative PCR revealed, furthermore, that the overall error rate (i.e. including allelic dropout and false allele) and the rate of positive PCR results (i.e. proportion of loci per samples that were successfully genotyped), which averaged at 80.0 ± 17%, did not depend on the DNA quantity in the analyzed faecal samples (overall error rate: N = 303, r = -0.03, p = 0.66; rate of positive PCR: N = 302, r = 0.07, p = 0.18; Fig. 3).

After the removal of unpromising samples or samples of known males that have not been observed during either of the two rutting seasons 353 genotypes remained in the data set. Identity analyses demonstrated that in total 70 kids (13 and 57 born in 2006 and 2007, respectively), 67 mothers and 100 males older than 1 year of age had been successfully genotyped on average 1.5 ± 0.9 (mean ± SD) times. For the paternity tests concerning the kids born in the two years, 62 and 84 males were considered, respectively. Comparisons of the genetic data and observations during the rut showed that 27 of 31 (87.1%) and 51 of 61 (83.6%) identifiable males which had been observed during the two rutting periods, had also been successfully sampled and genotyped. Remaining DNA samples of males in the data set originated from unidentifiable animals (aged 1-5 years) which had been sampled in the study area, and which were not unlikely to have participated in the reproduction during the two rutting seasons. Sampling and genotyping success corresponded in general well with the number of observed males in the different age classes (Fig. 1). Some divergence seemed to exist among males of 1-3 years of age. The 13 and 57 kids of which DNA samples entered the paternity analyses represented 68.4 % and 90.4% of the maximally observed kids during the consecutive fall / winter censuses in 2006 and 2007, respectively (see Table 1).

Pedigree reconstruction

Despite the differing parameterisation, the four models resulted overall in similar pedigrees. Hence, considering the posterior distribution of paternity, all models made the same assignments to particular kids in 91.4% at a confidence level of 80%, and in 81.4% at a confidence level of 95%. The few cases in which the four models did not match were entirely due to situations in which one or more models did not assign paternities, whereas others did. Accordingly, if kids were assigned a likely paternity in ≥ 2 models, in all these models always the same males were proposed as the likely fathers. Overall, the four models assigned likely fathers to 70-71% of the sampled kids at the confidence level of 80%, and to 55-63% of the kids at the 95% confidence level, respectively (Table 2). Hence, the different models performed roughly equally well. This impression is also reflected by the estimated number of unknown sires, which covered a similar range in all four models with medians between 7.9 and 11.2 males (Table 2).

Factors affecting paternity

Parameter estimates for the effects of age, dominance and tactic deviated all significantly from zero (Table 2). The two simplest models 1 and 2 containing age and age^2 as factors, hence demonstrated that the likelihood of siring offspring tended to augment with increasing age. The negative slope for age^2 in model 2 indicated, however, that after an age of 10-11 years the likelihood of siring offspring was decreasing again. The observed relationship between age and the mean number of paternities per male is illustrated in figure 4. The median in individual reproductive success did principally not increase before the age of 10 years, although variation among 7 and 8 year old individuals was already remarkable.

Among males ≤ 6 years of age, 0-13% of the individuals per age class were assigned ≥ 1 paternity compared to 27-100% in males aged 7-11 years (Table 3). In the age classes of the 12-13 years old animals no males were assigned ≥ 1 paternity.

Considering the two other models, the positive parameter estimates for dominance rank (model 3) and tactic index (model 4) suggested that high dominance and the adoption of the tending tactic to attain access to receptive females were important determinants of male reproductive success in Alpine ibex (Table 2). Hence, the number of sired offspring in our population increased considerably in animals that held dominance ranks above 0.60 and in which tactic indices surpassed 0.80 (Fig. 5). Lower-ranking males and males adopting less often the tending tactic only occasionally achieved to sire offspring. Medians close to zero indicate that the majority of them were ascribed no paternities at all.

As expected, paternities assigned to (supposedly not yet full-grown) males ≤ 7 years of age were mainly due to individuals adopting chiefly the coursing tactic (average tactic index: median = 0.14; 95% CI = 0.10 to 0.25; based on model 3), while assigned paternities among (supposedly full-grown males) of ≥ 8 years of age were mainly due to individuals adopting chiefly the tending tactic (average tactic index: median = 0.92; 95% CI = 0.90 to 0.95).

Variation in individual reproductive success and opportunity for selection

The mean number of assigned paternities per individual male of the offspring cohort in 2007, when a large portion of kids in the whole study population could be sampled (see above), based on the 1000 MCMC samples varied around 0.63-0.64 kids per male depending on the chosen model, with variances of 2.0 to 2.2. Estimates of I_m ranged accordingly between 4.8 and 5.6 (Table 2). When I_m was calculated based on the paternities assigned at the confidence level of 80% it even took on values between 7.1 and 8.0. Figure 6 shows that with on average about 60 males much more individuals than would be expected under random allocation produced no offspring during the rut in 2006-07; about 15 males sired one offspring, and about 10 males sired 2 or more offspring.

Discussion

The fact that 70-71% and 55-63% of the offspring could be assigned a likely father at the 80% and 95% confidence levels, respectively, and that these assignments did not principally differ between the differently parameterized models denoted that the information coming from the genetic data (which consisted largely of faecal samples) was in general sufficient to identify paternity in Alpine ibex. Nevertheless, the small discrepancies between the models highlighted also the utility and importance of ecological data to augment the power of paternity assignments when the information coming from the genetic material is not exhaustive (for details see Hadfield et al. 2006). Hence, in some cases, the low genetic diversity (which was the result of a bottleneck in the recent history of Alpine ibex; Biebach 2009) in our samples inhibited probably the successful distinction between possible candidate fathers at given confidence levels (see, for instance, O'Connor et al. 2006). As suggested by the estimated 7.9-11.2 unknown sires, some of the unassigned offspring at the 80% and 95% confidence levels were however likely to be due to incomplete sampling and genotyping of males. This impression is in accordance with the fact that we failed to collect or genotype successfully DNA samples of 12 known males which have been observed during the corresponding ruts (C.S. Willisch, unpublished data).

The results of the paternity analyses confirmed our hypothesis that reproductive success is heavily skewed towards older, tending males in Alpine ibex, while younger ones making predominately use of the parasitic coursing tactic sire only few offspring. Accordingly, all three variables age, tactic index and dominance rank, were shown to have strong effects on the likelihood of individual males to sire offspring. On average, highest reproductive success was achieved among (i) males aged 10-11 years, (ii) males holding dominance ranks above 0.8, and (iii) males having adopted in more than 80% of observations the tending tactic. The only exception in this regard was a 7 year old male that was ascribed on average >8 paternities, which is the highest success recorded for a single individual. As can already be suspected from figures 2 and 5, this male was highly dominant and made extensive use of the tending tactic, suggesting that it was a high quality male above age-specific average. Consistent with behavioural observations (Willisch and Neuhaus in press, submitted) and findings on reproduction in male bighorn sheep (Hogg and Forbes 1997), relative dominance (compared to present competitors) was apparently important among older, full-grown males to gain paternities via the tending tactic, whereas it appeared to provide no immediate advantages among younger, coursing males. In these males agility and running speed are thought to be the crucial determinants (Hogg and Forbes 1997; Willisch and Neuhaus in press), since only males that are able to outrun their competitors will have chances to mate with the receptive female during or following a coursing chase.

Regarding the effects of age, dominance rank and the adoption of alternative mating tactics on the reproductive success in male ungulates, the general trends detected in this study were also observed in other species whose survival rates were on average 6-30% lower than the ones found in Alpine ibex; i.e. bighorn sheep (Bonenfant et al. 2009), Soay sheep (Clutton-Brock et al. 1992), reindeer (Toigo and Gaillard 2003) or white-tailed deer (Ditchkoff et al. 2001). However, in none of these species reproductive success early in life was as low and sporadic as in Alpine ibex, supporting the second part of our hypothesis that reproductive investments at young age through sneaking tactics will be less important in species with high survival compared to species with lower survival. In bighorn sheep, for instance, males from 2-3 years of age onwards were reported to reproduce frequently via the coursing tactic (Coltman et al. 2002; Hogg and Forbes 1997), and they were even proved to be responsible for more than 40% of all assigned paternities in two populations (Hogg and Forbes 1997). In reindeer and white-tailed deer, males aged only 1 year were evidenced to successfully sire on average 0.37 and 1.3 offspring, respectively (Roed et al. 2005; Sorin

2004), while in Soay sheep, the species with the lowest reported survival (Clutton-Brock et al. 1992), common reproduction was confirmed to occur already among juvenile males (Coltman et al. 1999a; Coltman et al. 1999b). Only in male wood bison, *Bison bison*, reproduction appeared to be heavily skewed towards males ≥ 5 years of age, while younger ones did obviously not sire any offspring (Wilson et al. 2002). Males of this species, exhibited similar to male Alpine ibex a relatively high annual survival of 95% (Toigo and Gaillard 2003), corroborating our hypothesis that in animals with high survival reproduction early in life should be only of minor importance.

In agreement with the results presented in this study, behavioural observations revealed that young, coursing male Alpine ibex did obviously not make use of all their possibilities during the rut to obtain mating access to receptive females. Hence, it was observed that subordinate, coursing male Alpine ibex did not apply overt aggression against tending males (Willisch and Neuhaus in press, submitted), and that they spent overall only little time in activities (such as moving, courtship or agonistic behaviours; (Willisch and Neuhaus in press) that would have enhanced their chances to mate with females. This is at least suggested by the comparatively high reproductive success of aggressively (Hogg and Forbes 1997) competing young, coursing males in bighorn sheep and Soay sheep (Coltman et al. 1999a; Coltman et al. 1999b; Preston et al. 2001). Thus, compared to bighorn sheep and Soay sheep, in which coursing can be considered to be a high cost – high gain tactic (Hogg and Forbes 1997; Pelletier 2005; Preston et al. 2001), coursing in male Alpine ibex seemed to be rather a low cost – low gain tactic (Willisch and Neuhaus in press). Regarding the hypothesized trade-off between investments into current and into future reproduction, young male Alpine ibex therefore appeared to primarily minimize the risks of depressed growth and survival while preserving at the same time some minor chances to reproduce already early in life via the adoption of the coursing tactic.

Several studies already pointed out that reproductive effort in male ungulates may be changing with their age (e.g., Forsyth et al. 2005; Mainguy and Cote 2008; Mysterud et al. 2004; Mysterud et al. 2005) and with the adopted mating tactic (e.g., Pelletier 2005; Willisch and Neuhaus in press; Yoccoz et al. 2002). Because the phenotypic quality of individuals appears to play an important role with regard to the reproductive investments in polygynous male ungulates (McElligott et al. 2003; Pelletier et al. 2006), it would in a next step be worthwhile to look for individual variation in the trade-off between investments into current versus future reproduction. Thus, it might be interesting to investigate whether reproductive effort and the corresponding survival and reproduction perspectives at young age differ between males of differing quality. Based on life-history theory one should principally expect individuals that have bad perspectives to become a successful reproducer at an old age to invest relatively more energy into the coursing tactic at young age than individuals with good perspectives, since the latter risk to lose more when comprising their future survival or growth. However, the verification of such patterns might be particularly difficult in purely correlative studies, as life-history traits in individuals ungulates are often found to be positively correlated. Thus, Pelletier et al. (2006), for example, found a positive relationship between time investments in the coursing tactic and longevity in male bighorn sheep, while McElligott et al. (2002) demonstrated a positive relationship between reproduction and survival. Similarly, in male Alpine ibex, horn growth in one year was positively correlated with their subsequent survival perspectives (von Hardenberg et al. 2004) indicating that males of higher quality (see also von Hardenberg et al. 2007) might afford to grow longer horns while simultaneously exhibiting a better survival. In accordance with this, but in contrast to the above mentioned expectations, Bergeron et al. (2008) proposed that shot-horned, and thus poor quality males might increase their survival by limiting their reproductive effort.

The finding that reproductive success was largely (though not completely, as evidenced by the few paternities ascribed to young males) restricted to some older, high ranking males engaging primarily in the tending tactic, has consequentially led to a marked reproductive skew among males in the population. Thus, most of the males were not assigned any offspring, while high reproductive success was limited to only few animals in the population. Examination of I_m in other ungulates (summarized in table 4), furthermore, pointed out that reproductive skew in male Alpine ibex can be considered to be relatively high even when compared to other polygynous animals. The extent to which the behaviour of females affected the reproductive success and skew of male Alpine ibex is difficult to estimate. In comparison to females of lek breeding species (such as, for instance, fallow deer, *Dama dama*: Clutton-Brock et al. 1988; African topi, *Damaliscus lunatus*: Bro-Jorgensen 2002, 2007), receptive females in our study population appeared to have only limited possibilities to choose freely among potential mating partners, as typically the most dominant male in the group monopolized access to the receptive female by adopting the tending tactic (Willisch and Neuhaus in press, submitted). Nevertheless, behavioural observations indicate that females would have a certain potential to influence the paternity of their offspring. Thus, females seemed, for instance, capable of keeping unwanted males at distance by resorting to retreats (typically on small ledges of the cliffs; C.S. Willisch, pers. observation) that are difficult to access for males, making it virtually unfeasible for them to approach, mount and / or coerce copulations with females (see also (Bro-Jorgensen 2003). Another mechanism available to females might be the triggering of coursing chases. By doing so tended females might directly create copulation opportunities for subordinate, coursing males (Willisch and Neuhaus in press), as reported for bighorn sheep (Hogg 1984; Hogg and Forbes 1997). The fact that females involved in coursing chases were never observed to stop running in order to copulate ‘cooperatively’ with one or more pursuing males (C.S. Willisch, pers. observation) questions, however, the plausibility of this suspicion. The low rates of coursing chases and copulations to which receptive females were subject (Willisch and Neuhaus in press) furthermore indicate that sperm competition and cryptic female choice in Alpine ibex appear to be only of minor importance compared to the more promiscuously breeding bighorn sheep (Hogg and Forbes 1997) and Soay sheep (Preston et al. 2001). Clearly, further studies would be needed to shed more light on the role female mating behaviour in Alpine ibex.

Conclusions

The results of this study indicate that male Alpine ibex exhibited a rather unusual life-history strategy targeting for slow and prolonged growth, late reproduction and long life (see also, Toïgo et al. 2007). Young males appeared to prioritize investments into growth and survival at the expense of a relatively low reproductive success. Failing to reproduce successfully at young age by the adoption of the coursing tactic is however predicted to be outweighed at old age, when animals become dominant enough to monopolize access to receptive females via the tending tactic. ‘Slow’ life trajectories as the one described here for male Alpine ibex are expected to be rare among male ungulates, because they are likely to evolve only under environments allowing for a constantly high yearly survival. If survival is low for whatever reason (e.g., elevated predation pressure, climate change or hunting) selection for ‘faster’ life-history strategies will be likely to take place. In this context, an important result of this study was the finding that the reproductive skew, I_m, which is also referred to as the ‘opportunity for selection’ (Shuster and Wade 2003), was relatively high in male Alpine ibex. High values of I_m indicate that heritable traits in males can be subject of fast selection. This bears major implications for their management. Thus, if management plans will lead to selection processes favouring certain traits, which are important determinants of male reproductive success, relative quick changes in the frequency of these traits in the population will occur (Shuster and Wade 2003). In case that the human-induced selection processes favour the removal of animals with typically high reproductive potentials counter-evolutionary effects will sooner or later manifest (Coltman et al. 2003; Conover and Munch 2002; Harris et al. 2002).

Acknowledgements

We thank K. Bieri, P. Decristophoris, I. Glanzmann, N. Grandjean, B. Nussberger, Lena Senn, C. Wittker, and numerous volunteers for their assistance in data collection in the field. We thank L. Senn for her work in the laboratory, and E. Postma and P. Wandeler for their assistance with genetic and statistical analyses. Furthermore we appreciate the help of numerous people in capturing and marking Alpine ibex, above all J.-C. Roch, as well as K. Bieri, P. Deleury, C. Hebeisen, B. Hofer, I. Leathwood, H. Nimmervoll. We thank R. Bshary for valuable comments on the manuscript. We are particularly grateful to S. Sachot and J.-C. Roch of the Canton Vaud who permitted and supported the conduction of this study in the population of 'Cape au Moine' (VD). Financial support was provided by the Federal Office of the Environment (FOEN).

References

Bell, G. 1980. The costs of reproduction and their consequences, American Naturalist 116**:**45-76.

Bergeron, P., M. Festa-Bianchet, A. Von Hardenberg, and B. Bassano. 2008. Heterogeneity in male horn growth and longevity in a highly sexually dimorphic ungulate, Oikos 117**:**77-82.

Biebach, I. 2009. Genetic structure, genetic diversity and inbreeding in reintroduced Alpine ibex (*Capra ibex ibex*) populations. Dissertation, University of Zürich, Zürich.

Bonenfant, C., F. Pelletier, M. Garel, and P. Bergeron. 2009. Age-dependent relationship between horn growth and survival in wild sheep, Journal of Animal Ecology 78**:**161-171.

Bro-Jorgensen, J. 2002. Overt female mate competition and preference for central males in a lekking antelope, Proceedings of the National Academy of Sciences of the United States of America 99**:**9290-9293.

Bro-Jorgensen, J. 2003. No peace for estrous topi cows on leks, Behavioral Ecology 14**:**521-525.

Bro-Jorgensen, J. 2007. Reversed sexual conflict in a promiscuous antelope, Current Biology 17**:**2157-2161.

Bucher, T. 2007.Quantitative Bestimmung von Steinbock-DNS in Kotproben mittels Real-Time-PCR. Diplomarbeit, Universität Zürich, Zürich.

Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals, American Naturalist 123**:**212-229.

Clutton-Brock, T. H. 1988. Reproductive success. Studies of individual variation in contrasting breeding systems. The University of Chicago Press, Chicago.

Clutton-Brock, T. H., D. Green, M. Hiraiwa-Hasegawa, and S. D. Albon. 1988. Passing the buck: resource defence, lek breeding and mate choice in fallow deer, Behavioral Ecology and Sociobiology 23:281-296.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer. Behavior and ecology of two sexes. The University of Chicago Press, Chicago.

Clutton-Brock, T. H., O. F. Price, S. D. Albon, and P. A. Jewell. 1992. Early development and population fluctuations in Soay sheep, Journal of Animal Ecology 61:381-396.

Coltman, D. W., D. R. Bancroft, A. Robertson, J. A. Smith, T. H. Clutton-Brock, and J. M. Pemberton. 1999a. 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 Series B-Biological Sciences 269:165-172.

Coltman, D. W., P. O'donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting, Nature 426:655-658.

Coltman, D. W., et al. 1999b. Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams, American Naturalist 154:730-746.

Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales, Science 297:94-96.

Coté, S. D. 2000. Dominance hierarchies in female mountain goats: Stability, aggressiveness and determinants of rank, Behaviour 137:1541-1566.

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

De Vries, H., and M. C. Appleby. 2000. Finding an appropriate order for a hierarchy: a comparison of the I&SI and the BBS methods, Animal Behaviour 59:239-245.

De Vries, H., W. J. Netto, and P. L. H. Hanegraaf. 1993. Matman - A program for the analysis of sociometric matrices and behavioral transition matrices, Behaviour 125:157-175.

Ditchkoff, S. S., E. R. Welch, R. L. Lochmiller, R. E. Masters, and W. R. Starry. 2001. Age-specific causes of mortality among male white-tailed deer support mate-competition theory, Journal of Wildlife Management 65:552-559.

Dobson, F. S., and M. K. Oli. 2007. Fast and slow life histories of mammals, Ecoscience 14:292-299.

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

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and evolution of mating systems, Science 197:215-223.

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.

Gammell, M. P., H. De Vries, D. J. Jennings, C. M. Carlin, and T. J. Hayden. 2003. David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index, Animal Behaviour 66:601-605.

Hadfield, J. D., D. S. Richardson, and T. Burke. 2006. Towards unbiased parentage assignment: combining genetic, behavioural and spatial data in a Bayesian framework, Molecular Ecology 15:3715-3730.

Harris, R. B., W. A. Wall, and F. W. Allendorf. 2002. Genetic consequences of hunting: what do we know and what should we do? Wildlife Society Bulletin 30:634-643.

Harvey, P. H., and R. M. Zammuto. 1985. Patterns of mortality and age at 1st reproduction in natural populations of mammals, Nature 315:319-320.

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.

Johnson, P. C. D., and D. T. Haydon. 2007. Maximum-likelihood estimation of allelic dropout and false allele error rates from microsatellite genotypes in the absence of reference data, Genetics 175:827-842.

Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment, Molecular Ecology 16:1099-1106.

Komers, P. E., F. Messier, and C. C. Gates. 1992. Search or relax - the case of bachelor wood bison, Behavioral Ecology and Sociobiology 31:195-203.

Kozlowski, J. 1992. Optimal allocation of resources to growth and reproduction - implications for age and size at maturity, Trends in Ecology & Evolution 7:15-19.

Loison, A., J. M. Gaillard, C. Pelabon, and N. G. Yoccoz. 1999. What factors shape sexual size dimorphism in ungulates? Evolutionary Ecology Research 1:611-633.

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

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

Mainguy, J., S. D. Cote, E. Cardinal, and M. Houle. 2008. Mating tactics and mate choice in relation to age and social rank in male mountain goats, Journal of Mammalogy 89**:**626-635.

Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations, Molecular Ecology 7**:**639-655.

Maudet, C., G. Luikart, D. Dubray, A. Von Hardenberg, and P. Taberlet. 2004. Low genotyping error rates in wild ungulate faeces sampled in winter, Molecular Ecology Notes 4**:**772-775.

McElligott, A. G., R. Altwegg, and T. J. Hayden. 2002. Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*), Proceedings of the Royal Society of London Series B-Biological Sciences 269**:**1129-1137.

McElligott, A. G., and T. J. Hayden. 2000. Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*), Behavioral Ecology and Sociobiology 48**:**203-210.

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.

Morin, P. A., K. E. Chambers, C. Boesch, and L. Vigilant. 2001. Quantitative polymerase chain reaction analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*), Molecular Ecology 10**:**1835-1844.

Mysterud, A., R. Langvatn, and N. C. Stenseth. 2004. Patterns of reproductive effort in male ungulates, Journal of Zoology 264**:**209-215.

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.

O'connor, K. D., A. B. Marr, P. Arcese, L. F. Keller, K. J. Jeffery, and M. W. Bruford. 2006. Extra-pair fertilization and effective population size in the song sparrow *Melospiza melodia*, Journal of Avian Biology 37**:**572-578.

Oliveira, R. F., M. Taborsky, and H. J. Brockmann. 2008. Alternative reproductive tactics. An integrative approach. Cambridge University Press, Cambridge.

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

Pelletier, F., J. T. Hogg, and M. Festa-Bianchet. 2006. Male mating effort in a polygynous ungulate, Behavioral Ecology and Sociobiology 60:645-654.

Pemberton, J. M. 2008. Wild pedigrees: the way forward, Proceedings of the Royal Society B-Biological Sciences 275:613-621.

Pemberton, J. M., S. D. Albon, F. E. Guinness, T. H. Clutton-Brock, and G. A. Dover. 1992. Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal, Behavioral Ecology 3:66-75.

Pemberton, J. M., D. W. Coltman, J. A. Smith, and J. G. Pilkington. 1999. Molecular analysis of a promiscuous, fluctuating mating system, Biological Journal of the Linnean Society 68:289-301.

Pianka, E. R., and W. S. Parker. 1975. Age-specific reproductive tactics, American Naturalist 109:453-464.

Preston, B. T., I. R. Stevenson, J. M. Pemberton, and K. Wilson. 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.

Promislow, D. E. L., and P. H. Harvey. 1990. Living fast and dying young - a comparative-analysis of life-history variation among mammals, Journal of Zoology 220:417-437.

Ratti, P., and K. H. Habermehl. 1977. Investigations into age estimation and age-determination of mountain ibex (*Capra ibex ibex*) in kanton Graubunden, Zeitschrift für Jagdwissenschaft 23:188-213.

Roed, K. H., O. Holand, H. Gjostein, and H. Hansen. 2005. Variation in male reproductive success in a wild population of reindeer, Journal of Wildlife Management 69:1163-1170.

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.

Shuster, S. M., and M. J. Wade. 2003. Mating systems and strategies. Princeton University Press, Princeton.

Sorin, A. B. 2004. Paternity assignment for white-tailed deer (*Odocoileus virginianus*): Mating across age classes and multiple paternity, Journal of Mammalogy 85:356-362.

Stearns, S. C. 1976. Life-history tactics - review of ideas, Quarterly Review of Biology 51:3-47.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York.

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 Series B-Biological Sciences 262:267-275.

Stevenson, I. R., P. Marrow, B. T. Preston, J. M. Pemberton, and K. Wilson. 2004. Adaptive reproductive strategies.in Soay sheep. Dynamics and selection in a island population. (T. H. Clutton-Brock and J. Pemberton, eds.). Cambrigde University Press, Cambridge.

Taberlet, P., L. P. Waits, and G. Luikart. 1999. Noninvasive genetic sampling: look before you leap, Trends in Ecology & Evolution 14:323-327.

Taborsky, M. 1997. Bourgeois and parasitic tactics: do we need collective, functional terms for alternative reproductive behaviours? Behavioral Ecology and Sociobiology 41:361-362.

Taborsky, M., R. F. Oliveira, and H. J. Brockmann. 2008. The evolution of alternative reproudctive tactics: concepts and questions.in Alternative reproductive tactics. An integrative approach. (R. F. Oliveira, M. Taborsky and H. J. Brockmann, eds.). Cambrigde University Press, Cambridge.

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

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

Valiere, N. 2002. GIMLET: a computer program for analysing genetic individual identification data, Molecular Ecology Notes 2:377-379.

Vanpe, C., et al. 2008. Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate, Behavioral Ecology 19:309-316.

Von Hardenberg, A., B. Bassano, M. P. Z. Arranz, and G. Bogliani. 2004. Horn growth but not asymmetry heralds the onset of senescence in male Alpine ibex (*Capra ibex*), Journal of Zoology 263:425-432.

Von Hardenberg, A., B. Bassano, M. Festa-Bianchet, G. Luikart, P. Lanfranchi, and D. Coltman. 2007. Age-dependent genetic effects on a secondary sexual trait in male Alpine ibex, Capra ibex, Molecular Ecology 16:1969-1980.

Wehausen, J. D., R. R. Ramey, and C. W. Epps. 2004. Experiments in DNA extraction and PCR amplification from bighorn sheep feces: the importance of DNA extraction method, Journal of Heredity 95:503-509.

Williams, G. C. 1966. Natural selection costs of reproduction and a refinement of Lacks principle, American Naturalist 100:687-&.

Willisch, C. S., and P. Neuhaus. in press. Alternative mating tactics and their impact on survival in adult male Alpine ibex (*Capra ibex ibex*), Journal of Mammalogy.

Willisch, C. S., and P. Neuhaus. submitted. Social dominance and conflict reduction in male Alpine ibex (*Capra ibex*) during the rut, Behavioral Ecology and Sociobiology.

Wilson, G. A., W. Olson, and C. Strobeck. 2002. Reproductive success in wood bison (*Bison bison athabascae*) established using molecular techniques, Canadian Journal of Zoology - Revue Canadienne de Zoologie 80**:**1537-1548.

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

Yoccoz, N. G., A. Mysterud, R. Langvatn, and N. C. Stenseth. 2002. Age- and density-dependent reproductive effort in male red deer, Proceedings of the Royal Society of London Series B-Biological Sciences 269**:**1523-1528.

Figures

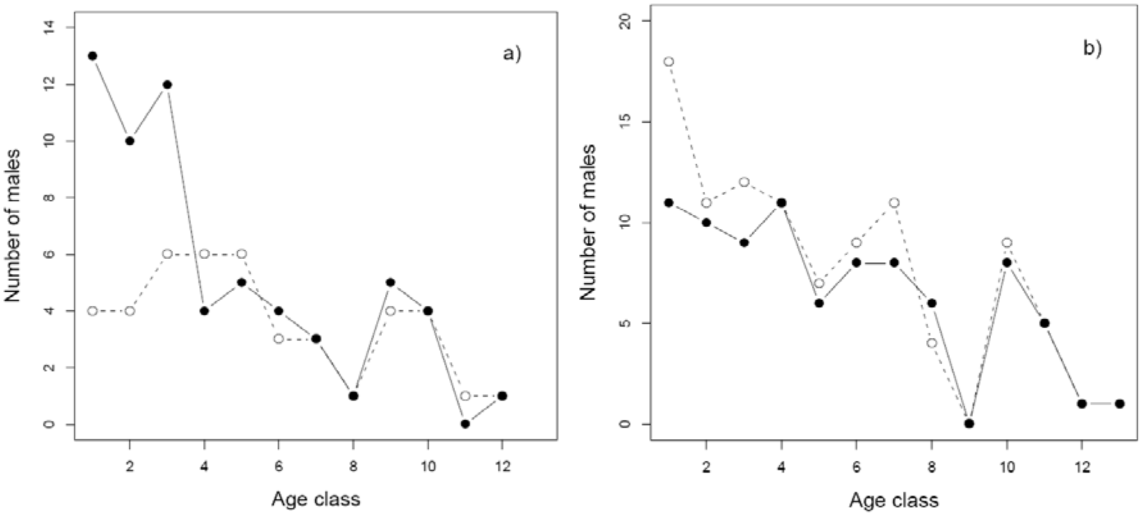

Fig. 1. Maximum number of observed males (open circles and dashed lines) during daily censuses in the rutting periods of 2005-06 (a) and 2006-07 (b), respectively, and the corresponding numbers of males that have been successfully sampled and genotyped (filled circles and solid lines).

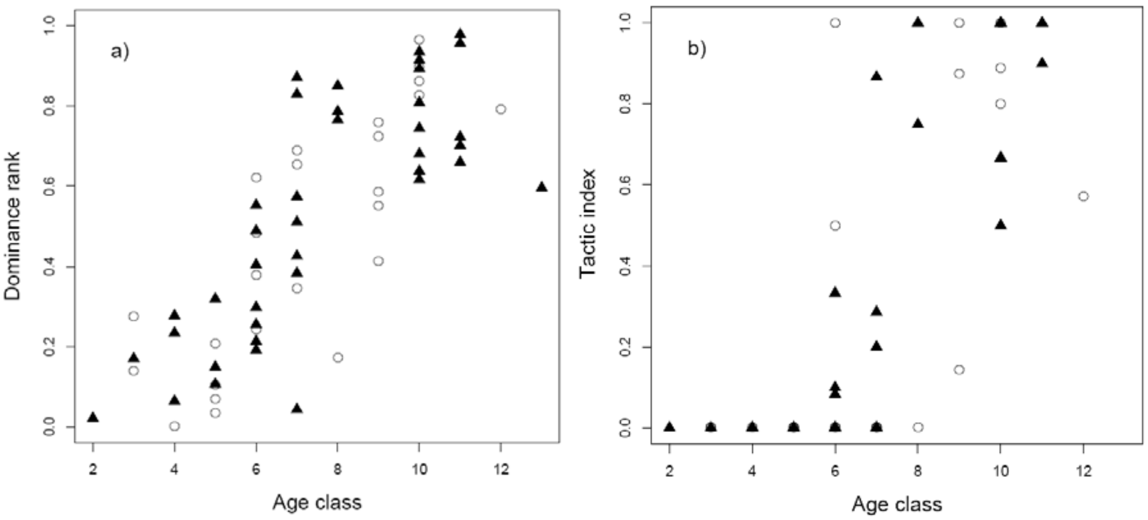

Fig. 2. Relationship between age and dominance rank (a) and age and tactic index (b) of individual males during the pre-rut and rutting seasons in 2005-06 (open circles) and 2006-07 (closed triangles).

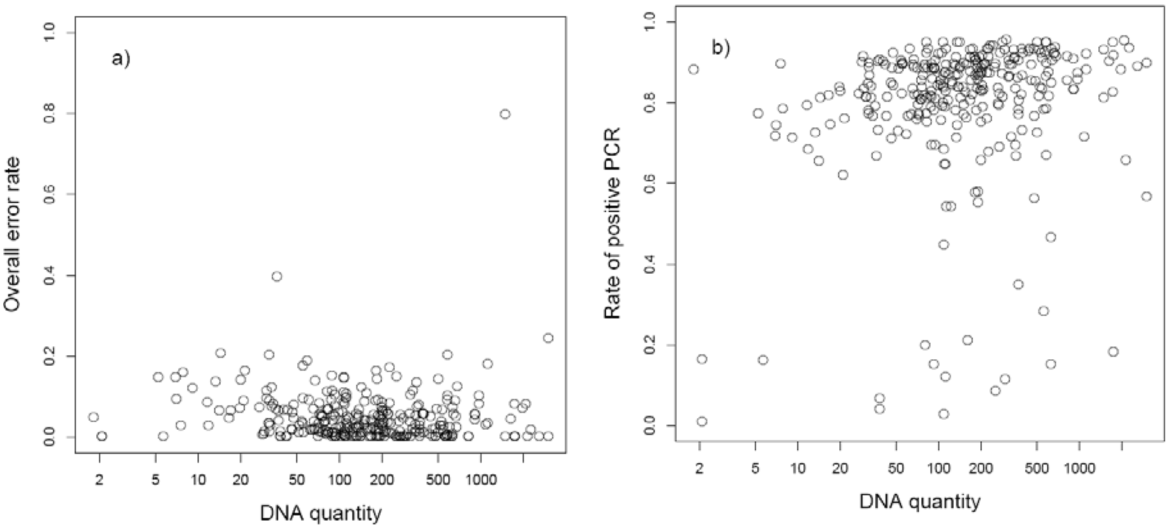

Fig. 3. (a) Overall error rate (sum of allelic dropout, false allele) and (b) rate of positive PCR across the genotyped loci in relation to the detected DNA-quantities (pg/µl; logarithmic scale) in the investigated faecal samples.

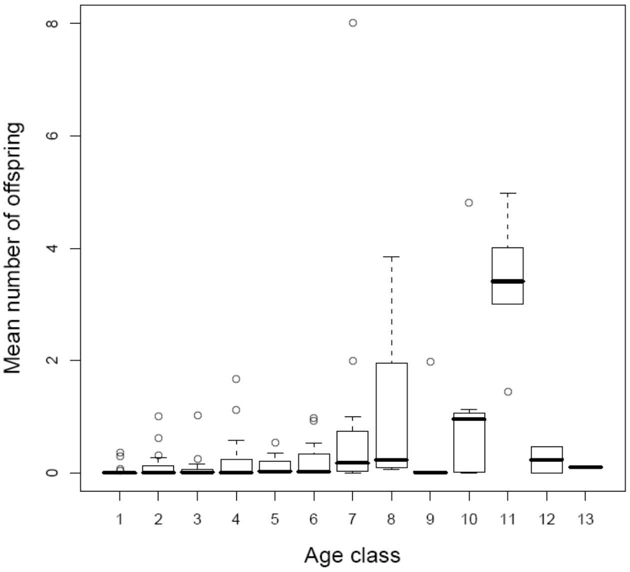

Fig. 4. Box-plot of the mean number of offspring per individual male (offspring cohorts 2006 and 2007 pooled) in relation to the age of males during the preceding ruts, based on the posterior distribution of the 1000 MCMC sample pedigrees of model 1.

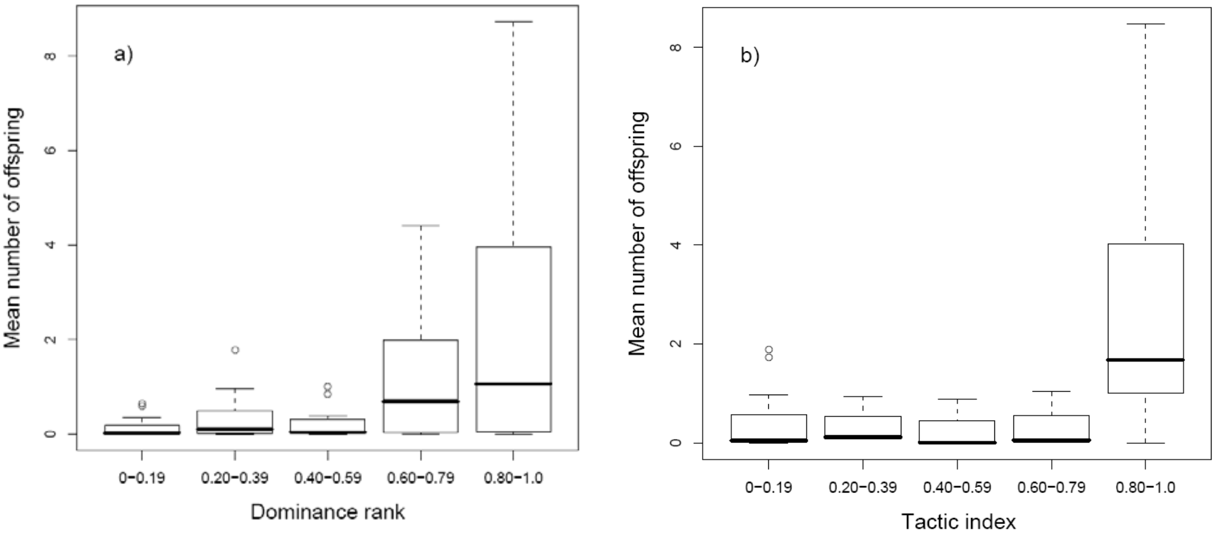

Fig. 5. Box-plots of the mean number of offspring per individual male (offspring cohorts 2006 and 2007 pooled) in relation to the dominance ranks (a) and tactic indices (b) of males during the preceding ruts, based on the posterior distribution of the 1000 MCMC sample pedigrees of model 3 and 4, respectively.

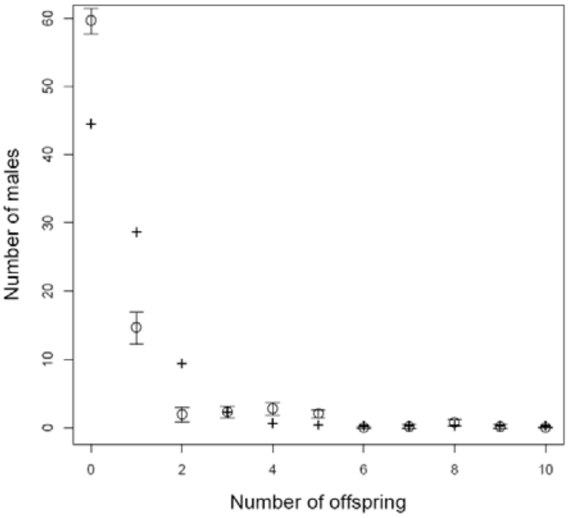

Fig. 6. The observed distribution of assigned paternities (open circles; mean ± SD) of the offspring cohort in 2007 among 84 males that were present during the preceding rut and the expected distribution of paternities under random assignment (plus signs), based on the 1000 MCMC samples of the posterior distribution of the pedigree of model 1.

Tables

Table 1: Animal numbers, kid-female ratios and sex ratios in the study area based on animal censuses conducted in 2005-06, 2006-07, and 2007-08, respectively.

	Year	N	Total mean (± SD), max	Males mean (± SD), max	Females mean (± SD), max	Kids mean (± SD), max	Kid-female ratio mean (± SD)	Sex ratio (m/f) mean (± SD)
Subpopulation only [a]	Rut / pre-rut 2005-06	38	57.6 (14.5), 78	17.3 (6.0), 29	29.1 (7.8), 40	11.2 (3.4), 17	0.39 (0.09)	0.62 (0.19)
	Fall / winter 2006-07	27	66.9 (22.2), 104	24.5 (7.5), 38	31.0 (12.3), 56	11.73 (4.0), 19	0.37 (0.15)	0.86 (0.27)
Whole population [b]	Rut / pre-rut 2006-07	13	194.8 (21.2), 221	67.8 (9.5), 81	89.6 (10.9), 111	36.6 (3.8), 42	0.41 (0.04)	0.76 (0.10)
	Fall / Winter 2007-08	5	255 (13.23), 266	84.4 (6.5), 95	109.4 (9.6), 120	61.0 (2.5), 63	0.56 (0.04)	0.77 (0.09)

a: Only a part of the population monitored. The relatively high variation (compared to the estimates covering the whole study area) in the corresponding census data is likely to be caused by a group of nearby animals that occasionally entered this area.

b: Whole population monitored. Because of the size of the study area animal censuses spread over two consecutive days with safe snow conditions explaining the small sample sizes.

Table 2. Population-level parameters estimated from differently parameterized models (1-4) using MasterBayes. Explanatory variables are age (A), dominance rank (D) and tactic index (T) of males during the corresponding rutting seasons. MD and MT are secondary binary variables (missing vs. non-missing) that were fitted to account for missing dominance ranks and missing tactic indices in the data set, respectively. Estimates are based on the 1000 MCMC samples of the posterior distribution of the pedigree. Presented values are medians followed by the 95% credible intervals in brackets.

Model	Factor	Effect size	Number of assigned paternities at the 80% and 95% confidence level	Number of unknown sires	Average offspring number per male[a]	Average variance in offspring number per male[a]	I_m^{a}	$I_m^{a,b}$ based on assigned paternities at the 80% confidence level
Model 1								
A	A	0.27 (0.20 to 0.37)	50 and 42	8.6 (1.7 to 22.7)	0.64(0.60 to 0.68)	2.0 (1.7 to 2.3)	4.8 (4.2 to 5.7)	8.0
Model 2								
$A + A^2$	A	1.14 (0.55 to 1.98)	50 and 42	7.9 (1.7 to 21.6)	0.64 (0.60 to 0.67)	2.1 (1.8 to 2.3)	5.0 (4.3 to 5.7)	7.1
	A^2	-0.05 (-0.11 to -0.02)						
Model 3								
A + D + MD + A * MD	A	-0.11 (-0.26 to 0.05)	49 and 44	11.2 (4.5 to 21.7)	0.63 (0.57 to 0.67)	2.2 (1.9 to 2.5)	5.6 (4.7 to 6.7)	7.5
	D	4.26 (2.51 to 6.10)						
	MD	-0.23 (-2.50 to 2.11)						
	A * MD	-0.24 (-8.25 to 0.36)						
Model 4								
A + T + MT + A * MT	A	-0.09 (-0.26 to 0.07)	49 and 39	11.2 (4.5 to 24.5)	0.63 (0.57 to 0.67)	2.1 (1.9 to 2.5)	5.4 (4.7 to 6.6)	7.4
	T	2.61 (1.65 to 3.85)						
	MT	-2.16 (-4.10 to 0.30)						
	A * MT	0.24 (-4.68 to 0.49)						

a: Only offspring cohort 2007 considered.

b: In studies in which paternities have been inferred using molecular methods I_m is often derived from paternities assigned at the 80% confidence level (e.g., Coltman et al. 1999b; Vanpe et al. 2008).

Table 3. Number and proportion of males per age class that were assigned on average ≥ 1 paternity (offspring cohorts 2006 and 2007 pooled).

Age class	Number of males per age class	Number of males ≥ 1 paternity	Proportion of males ≥ 1 paternity
1	24	0	0.00
2	20	1	0.05
3	21	1	0.05
4	15	2	0.13
5	11	0	0.00
6	12	0	0.00
7	11	3	0.27
8	7	2	0.29
9	5	1	0.20
10	12	6	0.50
11	5	5	1.00
12	2	0	0.00
13	1	0	0.00

Table 4. Reproductive skew in different ungulates species, calculated as I_m. Because in some studies neither I_m nor the mean reproductive success and the variance were explicitly reported, we estimated these values by the use of the available distributions of reproductive success. Values calculated in this way are indicated by an '*'. Calculation method: L: Estimate is derived from life time breeding success; P: Estimate is derived from multiple, but pooled seasons; S: Estimate is derived from one breeding season; SA: Estimate is average from multiple seasons. The number of sampled offspring cohorts is shown in brackets.

Species	I_m	Calculation method	References
Bison bison	1.22*	P (4)	Wilson et al. 2002
	0.54[b]	SA (4);	Wilson et al. 2002
Capreolus capreolus	2.45*	P (18)	Vanpe et al. 2008
	0.75	L (18)	Vanpe et al. 2008
Cervus elaphus	2.51[a]	L	Clutton-Brock 1988
Dama dama	5.74*[b]	SA (3)	Say et al. 2003
Odocoileus virginianus	1.85*	S (1)	Sorin 2004
Ovis aries	4.0; max 6.9	SA (11)	Coltman et al. 1999b
	2.57	L (11)	Pemberton et al. 1999
Ovis canadensis	4.5; max 8.3	SA (6)	Coltman et al. 2002

a: Reproductive success based on behavioural estimates that had been shown to reflect reliably relative reproductive success among males (Pemberton et al. 1992).

b: Breeding males only, i.e. males having sired ≥ 1 offspring.

Appendix 1. Locus-specific error rates in genotyped faecal samples calculated using GIMLET. Corresponding data for blood and tissue samples was calculated by Biebach (2009) for a larger data set using PEDANT.

		Faecal samples		Blood and tissue samples	
Locus	# Alleles	Dropout rate	False allele rate	Dropout rate	False allele rate
BM1258	5	0.009	0.000	0.000	0.000
BM1818	2	0.113	0.012	0.026	0.000
BM302	4	0.014	0.006	0.000	0.000
BM415	2	0.035	0.031	0.000	0.000
BM4208	4	0.007	0.018	0.009	0.000
BM4505	2	0.203	0.033	0.074	0.000
CSSM47	3	0.016	0.005	0.071	0.000
ETH10b	2	0.058	0.002	0.019	0.000
HAUT27	3	0.122	0.029	0.020	0.000
ILSTS029	2	0.054	0.061	0.000	0.005
INRABERN175	2	0.064	0.038	0.010	0.000
JMP29	3	0.010	0.006	0.025	0.000
Maf209	3	0.000	0.000	0.000	0.000
MAF36	3	0.014	0.010	0.000	0.000
MAF70	2	0.041	0.004	0.000	0.000
McM152	4	0.003	0.004	0.000	0.000
McM73	4	0.011	0.025	0.000	0.000
MILSTS076	5	0.028	0.021	0.000	0.000
OarAE54	2	0.065	0.008	0.071	0.000
OARFCB193	6	0.017	0.012	0.000	0.000
OARFCB20	2	0.006	0.000	0.000	0.000
OarFCB48	2	0.020	0.007	0.000	0.000
OarHH35	3	0.318	0.049	0.000	0.000
OarHH62	3	0.126	0.031	0.011	0.000
OarkP6	2	0.019	0.007	0.000	0.000
OarVH34	2	0.026	0.006	0.000	0.000
SR-CRSP23	2	0.026	0.022	0.000	0.000
SR-CRSP07	2	0.158	0.004	0.000	0.000
SR-CRSP25	3	0.015	0.018	0.025	0.000
TGLA10	3	0.010	0.007	0.000	0.000
TGLA126	3	0.029	0.009	0.000	0.000
URB058	2	0.017	0.018	0.000	0.000
Mean (± SD)	2.88 (1.07)	0.052 (0.069)	0.016 (0.015)	0.011 (0.022)	0.000 (0.001)

CONCLUSION

This thesis is the first to provide reliable quantitative data on reproduction of male Alpine ibex. It is demonstrated that their reproductive behavior resembled in its major trends the reproductive behavior reported in other polygynous ungulates (e.g., Coltman et al. 2002; Coltman et al. 1999; Hogg & Forbes 1997; Roed et al. 2005; Sorin 2004). Accordingly, in male Alpine ibex important determinants of reproductive success were age, dominance rank and the adoption of alternative mating tactics. Nevertheless, Alpine ibex differed in some essential aspects from most of the other ungulates for which comparative data was available. The detected differences were all likely to be the outcome of an uncommon life-history strategy exhibited by male Alpine ibex which is characterized by high survival (Toïgo et al. 2007) and a slow, prolonged growth (Lüps et al. 2007). Most importantly, our results suggested that male Alpine ibex had to attain a high absolute age and dominance rank before being able to reproduce really successfully by the adoption of the tending tactic (compare with Coltman et al. 2002; Coltman et al. 1999; Hogg & Forbes 1997; Roed et al. 2005; Sorin 2004). This apparently affected considerably the cost-benefit trade-offs of young males, as they reduced remarkably their investments into current reproduction resulting in the observed low cost – low gain tactic coursing and the specific social system in which disputes over access to receptive females were resolved without the necessity of escalating interactions. As a consequence of the conservative behavior of young, coursing males a comparatively high reproductive skew towards older males in the population emerged, while younger individuals only sporadically succeeded in siring offspring.

In conclusion, this thesis points out that the reproductive behavior and the social system of polygynous males can vary greatly among species exhibiting differing life-history strategies. In agreement with life-history theory (Stearns 1992), the findings reported here denote, particularly, that in polygynous male ungulates with high survival and slow, prolonged growth investments into reproduction via sneaking tactics at young are likely to be less important than in species in which survival perspectives are worse.

The results presented in this thesis bear, however, also important implications for the active management of this species. Since survival, growth and reproduction are the key determinants of various life-history strategies in animals (Stearns 1992) their specific expression differentiate Alpine ibex from other ungulates. Therefore these aspects have to be taken seriously into account when establishing management plans. Managers have furthermore to be aware of the fact that male reproductive success is likely to be strongly skewed leading to a high opportunity for selection (Shuster & Wade 2003). If management plans will lead to selection processes favouring certain traits, which are important determinants of male reproductive success, relative fast changes in the frequency of these traits in the population have to be expected. In case that the selection processes favour the early removal of individuals with typically high reproductive potentials counter-evolutionary effects will manifest (Coltman et al. 2003; Conover & Munch 2002; Harris et al. 2002). With respect to the long evolved specific life history traits of male Alpine ibex, we, therefore, strongly advise managers not to select against longevity, prolonged growth or late reproduction in male Alpine ibex.

References

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

Coltman, D. W., O'Donoghue, P., Jorgenson, J. T., Hogg, J. T., Strobeck, C. & Festa-Bianchet, M. 2003: Undesirable evolutionary consequences of trophy hunting. Nature **426**, 655-658.

Coltman, D. W., Smith, J. A., Bancroft, D. R., Pilkington, J., MacColl, A. D. C., Clutton-Brock, T. H. & Pemberton, J. M. 1999: Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. American Naturalist **154**, 730-746.

Conover, D. O. & Munch, S. B. 2002: Sustaining fisheries yields over evolutionary time scales. Science **297**, 94-96.

Harris, R. B., Wall, W. A. & Allendorf, F. W. 2002: Genetic consequences of hunting: what do we know and what should we do? Wildlife Society Bulletin **30**, 634-643.

Hogg, J. T. & Forbes, S. H. 1997: Mating in bighorn sheep: Frequent male reproduction via a high-risk "unconventional" tactic. Behavioral Ecology and Sociobiology **41**, 33-48.

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 zur Jagd- und Wildforschung **32**, 495-510.

Roed, K. H., Holand, O., Gjostein, H. & Hansen, H. 2005: Variation in male reproductive success in a wild population of reindeer. Journal of Wildlife Management **69**, 1163-1170.

Shuster, S. M. & Wade, M. J. 2003: Mating systems and strategies. Princeton University Press, Princeton.

Sorin, A. B. 2004: Paternity assignment for white-tailed deer (*Odocoileus virginianus*): Mating across age classes and multiple paternity. Journal of Mammalogy **85**, 356-362.

Stearns, S. C. 1992: The evolution of life histories. Oxford University Press, New York.

Toïgo, C., Gaillard, J. M., 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. Journal of Animal Ecology **76**, 679-686.

ACKNOWLEDGMENTS

This thesis would not have been possible without the support and help of numerous people. I wish to thank all of them.

For the supervision I would like to express my gratitude to Peter Neuhaus. He enabled the conduction of this study at the University of Neuchâtel and provided essential support through all stages of the thesis.

For helpful advice, comments and discussions I wish to thank also the other members of our group, especially Redouan Bshary, Ralph Bergmüller, Shirley Raveh and Erica van de Waal. Brigitte Cattin and Roberta Ventura I would like to thank for their help in administrative matters.

Then, I would like to thank my assistants Paola Decristophoris, Katrin Bieri, Isabelle Glanzmann, Blaise Hofer, Noémie Grandjean, and Christian Wittker, as well as the volunteers Fabien Mavrot, Beatrice Nussberger, Sonja Stutz and Gregor Wittwer. They enjoyed and endured with me mostly long and sometimes harsh days in the field and contributed substantially to this thesis. I also appreciated the collaboration with the Master students Chanson Camille, Fanny Gosselin, Lena Senn and Martina Spinelli who were also working on Alpine ibex at ‘Cape au Moine’.

I am particularly grateful to the regional game warden, Jean-Claude Roch, whose personal commitment and effort especially regarding the captures of Alpine ibex at ‘Cape au Moine’ was indispensable for the realisation of this thesis. I would like to thank him also for his assistance and generosity in countless other situations, and for his good sense of humour. In addition, I appreciated as well the essential help provided by his colleagues, namely Patrick Deleury, Philippe Allamand, Shirley Berrios, Gabriel Bolomey, as well as Denis Combremont, and Philippe Mottier.

I would like to thank especially Marie-Pierre Ryser-Degiorgis and Nelson Marreros, as well as Helena Nimmervoll, Ilinka Leathwood, Christian Hebeisen and the numerous volunteers of the Centre for Fish and Wildlife Health, University of Berne for helping us with the capturing of Alpine ibex. Without them the marking of so many animals in the study area would not have been possible. Moreover, Marie-Pierre Ryser-Degiorgis was largely responsible for the sensible and well-organized capturing policy in our project which always targeted the well-being of the animals and humans. I appreciated that very much.

Special thanks go also to Lukas Keller, Iris Biebach, Thomas Bucher, Ursina Koller and Lena Senn of the Zoological Museum, University of Zurich for the establishment and performance of the challenging and tedious genetic analyses in the laboratory and the fundamental assistance with the subsequent paternity analyses. At the same time, I wish to thank also the other members of their group, especially Peter Wandeler and Erik Postma for valuable advice and discussions, as well as Barbara Oberholzer for the good collaboration with regard to financial matters.

I also would like to thank Matrin Zuber and Rolf Zumbrunnen of the Canton Berne, as well as Peter Lüps of the Natural History Museum of Berne. They provided me crucial information on the animals shot in the two adjacent populations 'Wittenberg' and 'Gummfluh', and they gave me the opportunity to investigate the corresponding skulls. Furthermore, Peter Lüps helped me with the age determination of photographed animals.

Many thanks to Jarrod Hadfield who helped me with the paternity analyses using MasterBayes, as well as to Han de Vries who provided useful advice regarding the handling of dominance data.

For their constructive comments and the valuable discussions I would like to thank the two external examiners Alan McElligott of the Queen Mary University of London, and Michael Taborsky of the University of Berne.

Many thanks to Erich Bächler, Bernhard Willisch and the association WildARK for the equipment placed at our disposal.

Further thanks also to Sebastien Sachot of the Canton Vaud, as well as Reinhard Schnidrig-Petrig, Sabine Herzog and Nicole Imesch of the Federal Office of the Environment (FOEN), for permitting and supporting this study in the population of 'Cape au Moine'. Thanks for financial support provided by the FOEN.

I am particularly grateful to my parents Bernhard and Ursula Willisch and my brother Thomas Willisch for their big and never-ending interest and support throughout the whole thesis.

For participating so intensively and closely in my work and for sharing all the ups and downs of the thesis I would like to thank especially my beloved partner Katrin Bieri. Her active help in the field, the possibility to discuss all the topics and problems related to the thesis in depth with her, as well as her enduring patience and support meant a lot to me and were essential for the realisation of this thesis.

Finally, I would like to thank all the known and unknown Alpine ibex at ‘Cape au Moine’ for offering me fascinating insights into their lives.