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Male reproductive pattern in a polygynous ungulate with a slow life-history: the role of age, social status and alternative mating tactics

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

Abstract According to life-history theory age-dependent investments into reproduction are thought to co-vary with survival and growth of animals. In polygynous species, in which size is an important determinant of reproductive success, male reproduction via alternative mating tactics at young age are consequently expected to be the less frequent in species with higher survival. We tested this hypothesis in male Alpine ibex (*Capra ibex*), a highly sexually dimorphic mountain ungulate whose males have been reported to exhibit extremely high adult survival rates. Using data from two offspring cohorts in a population in the Swiss Alps, the effects of age, dominance and mating tactic on the likelihood of paternity were inferred within a Bayesian framework. In accordance with our hypothesis, reproductive success in male Alpine ibex was heavily biased towards older, dominant males that monopolized access to receptive females by adopting the 'tending' tactic, while success among young, subordinate males via the sneaking tactic 'coursing' was in general low and rare. In addition, we detected a high reproductive skew in male Alpine ibex, suggesting a large opportunity for selection. Compared with other ungulates with higher mortality rates, reproduction among young male Alpine ibex was much lower and more sporadic. Consistent with that, further examinations on the species level indicated that in polygynous ungulates the significance of early reproduction appears to decrease with

C. S. Willisch (✉) · I. Biebach · U. Koller · T. Bucher · L. F. Keller
Institute of Evolutionary Biology and Environmental Studies, University of Zurich,
Winterthurerstrasse 190, 8057 Zurich, Switzerland
e-mail: willichristian@yahoo.com

C. S. Willisch · P. Neuhaus
Department of Eco-Ethology, Institute of Biology, University of Neuchâtel,
Emile-Argand 11, 2009 Neuchâtel, Switzerland

N. Marreros · M.-P. Ryser-Degiorgis
Centre for Fish and Wildlife Health, Vetsuisse Faculty, University of Bern,
Länggass-Strasse 122, 3001 Bern, Switzerland

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

increasing survival. Overall, this study supports the theory that survival prospects of males modulate the investments into reproduction via alternative mating tactics early in life. In the case of male Alpine ibex, the results indicate that their life-history strategy targets for long life, slow and prolonged growth and late reproduction.

Introduction

Because energy is a limited resource that has set important constraints under which life has evolved, 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 (Williams 1966; Stearns 1976). Investments into reproduction are costly and 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 (Pianka and Parker 1975; Clutton-Brock 1984).

In animals, in which size is an important determinant of reproductive success, individuals are principally assumed to first direct their investments into growth and survival before starting with reproduction. On the other hand, life-history theory also suggests that animals modulate the timing of reproduction with regard to their chances to reach full adult body size (Stearns 1992). Consistent with this, meta-analyses of female life-history traits in a variety of vertebrate species revealed that growth and survival both co-varied with reproduction in female animals: long life was associated with slow growth, delayed age of maturity, and late onset and low rates of reproduction, whereas short life was found to be associated with fast growth, early maturity and start of reproduction (Harvey and Zammuto 1985; Promislow and Harvey 1990; Dobson and Oli 2007). Thus, life-history strategies are distributed along a 'fast-slow' continuum (Stearns 1983).

Although equivalent studies for male vertebrates are still missing (presumably because reliable, molecular data on male reproductive success is not yet available for many vertebrate species), the interplay between growth, survival and reproduction, as predicted by life-history theory (Stearns 1992), should also apply to males. However, among male polygynous ungulates a rather distinct relationship between the different life-history traits might be expected because (1) direct male-male competition leads to strongly size-dependent access to female mating partners and thus reproductive success in these species (Isvaran 2005), and (2) mating activities are often associated with increased risks of injury or death (e.g. Clutton-Brock et al. 1982; Preston et al. 2001). Hence, male ungulates have to carefully trade their investments into current reproduction (given the risks involved) against investments into growth and survival in order not to jeopardize their future reproductive success.

In this study, we investigated age-dependent reproduction in male Alpine ibex (*Capra ibex*)—a highly sexually dimorphic and polygynous male mountain ungulate. Male Alpine ibex are supposed to pursue a rather slow life-history strategy, with prolonged growth, not reaching asymptotic body size until the age of 8 years (Lüps et al. 2007), and with a very high annual adult survival that exceeds survival of other ungulate species by 5–20% (Toïgo et al. 2007). Life-history theory predicts that reproductive success among male Alpine ibex should therefore be heavily skewed towards older individuals, with young males having little success. Although older males are also expected to have increased access to females

in ungulates with faster life-histories (Isvaran 2005) we expected male reproductive success to be more heavily biased towards older individuals in Alpine ibex than in these other species. Male Alpine ibex can adopt two different mating tactics during the rut (Willisch and Neuhaus 2009), but only dominant (typically older and fully grown; see also Bergeron et al. 2010) males are able to monopolize access to receptive females by the use of a so-called 'tending' tactic. Subordinate individuals have to make use of an alternative mating tactic termed 'coursing' to obtain transient mating access to females (Willisch and Neuhaus 2009, 2010). Consequently, we expected reproductive success in male Alpine ibex to be strongly biased toward dominant individuals making use of the tending tactic while subordinates using the coursing tactic were expected to be much less successful. To test these predictions we performed paternity analyses using DNA samples from two offspring cohorts and their mothers and potential fathers in an Alpine ibex population in the Swiss Alps, and estimated the effects of age, dominance, and mating tactics on reproductive success using a Bayesian framework. In addition, we compared our results with equivalent data from other polygynous ungulates.

Materials and methods

Study animals

The study was carried out between 2005 and 2008 in the Alpine ibex population 'Cape au Moine' north of Les Diablerets (VD), Switzerland. For details on this population of up to 270 animals (Table 1); see Willisch and Neuhaus 2009). During the study, up to 68 males (>2 years old) and 18 females (>2 years old) could be individually recognized based on unique characteristics of their horns and their coat coloration. Another 30 animals (20 males, and 10 females) were individually marked using colored and numbered ear tags (Willisch and Neuhaus 2009). The age of males was determined by counting the conspicuous horn annuli (Ratti and Habermehl 1977) either when captured or by inspection of photographs taken in the field (Willisch and Neuhaus 2009).

Alpine ibex are highly sexually dimorphic animals (average weight of fully grown males and females: 95 and 45 kg, respectively; Loison et al. 1999). In males, asymptotic body size is normally not reached until the age of 8 years (Lüps et al. 2007). Average annual survival of males in an unharvested population was extremely high, exceeding 98% in animals aged 2–8 years, and 85 and 97%, respectively, in animals aged 8–13 years depending on ecological conditions (Toïgo et al. 2007). As mentioned above, male Alpine ibex adopt two alternative mating tactics during the rut: a primary tactic termed 'tending', which is used by dominant and mainly older males in the population to monopolize access to receptive females, and a sneaking tactic termed 'coursing', which is typically adopted by subordinate, younger males to obtain temporary mating opportunities with tended females (Willisch and Neuhaus 2009, 2010).

Behavioural observations during the rut

Between November and January in 2005–2006 and 2006–2007 behavioural observations on individually identifiable male Alpine ibex were carried out in order to obtain (1) data on their dominance status, and (2) data on mating tactics.

To establish dominance hierarchies among males during the rut we constructed dyadic winner-loser matrices using the so called 'I & SI' method (De Vries 1998). Only animals

Table 1 Animal numbers, kid-female ratios and sex ratios (male per female) in the study area based on censuses conducted in 2005–2006, 2006–2007, and 2007–2008, respectively

	Season	N	Total [mean (±SD), max]	Males [mean (±SD), max]	Females [mean (±SD), max]	Kids [mean (±SD), max]	Kid-female ratio [mean (±SD)]	Sex ratio [mean (±SD)]
Subpopulation only[a]	Pre-rut/rut 2005–2006	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 2006–2007	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]	Pre-rut/rut 2006–2007	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 2007–2008	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] In the first year, only a part of the population was monitored

[b] Whole population monitored

which interacted with at least 5 other individuals were included in the data sets (2005–2006: 23 males; 2006–2007: 47 males). In male-male dyads individuals were the designated winners of agonistic encounters when they displaced or mounted their opponents, or when they were seen following their opponents after a fight. In addition, we also used the winner-loser information derived from situations in which males were competing for access to receptive females, as they were previously shown to reflect reliably the dominance relationships among males (Willisch and Neuhaus 2010). Linearity tests were conducted to test for deviations from linear hierarchies using Matman 1.1 (Noldus; De Vries et al. 1993). Afterwards, individuals were reordered to fit a linear hierarchy and assigned standardized ranks that varied between 0 (lowest ranking male) and 1 (highest ranking male; see Coté 2000).

The use of mating tactics was quantified using tactic indices calculated for each individual in each rutting period, 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 could range from 0 (male adopted exclusively the coursing tactic) to 1 (male adopted exclusively the tending tactic). For each male only the first observation per defended female and day was considered in order to avoid pseudo-replication.

Census data

Between 2005 and 2008 daily censuses were carried out between November and January to obtain information on the size and the sex-age structure of the population and the presence of individual males during the rut.

Genetic data

Between 2005 and 2008 we collected DNA samples of kids born in 2006 and 2007, and samples of their mothers and potential fathers. 651 DNA samples were gathered by collecting fresh faeces of individually recognizable animals. Since faecal samples vary in DNA quality, we sampled animals multiple times. An additional 43 blood and 54 tissue samples were obtained from animals by biopsy-darting (Biebach and Keller 2009), or from animals that were captured, 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.

Extraction of DNA from blood and tissue samples was performed as described in Biebach and Keller (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 extractions were carried out in a separate pre-PCR laboratory to avoid contamination with PCR products. All DNA samples were genotyped at 32 microsatellite loci (Appendix) in a separate post-PCR laboratory. Each 96-well plate contained one negative control to monitor contamination. We used PCR conditions and multiplex reactions as described in Biebach and Keller (2009) with the following two modifications for the faecal samples: 1) We used always 36 amplification cycles and 2) 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 LIZ size standard and the software GENEMAPPER 3.7 (Applied Biosystems) followed by

manual proofreading (Biebach and Keller 2009). All faecal samples were genotyped ≥3 times to account for increased genotyping error rates due to the low quality and quantity of DNA (Taberlet et al. 1999; Wehausen et al. 2004). The software package GIMLET (Valiere 2002) was used to build consensus genotypes when at least two of the three replicates produced consistent results. Samples not generating genotypes were repeated at least once. If replications failed to produce positive results, another sample of the same individual, if available, was analysed. We estimated locus-specific error rates in faecal samples using GIMLET (Appendix). Locus-specific error rates for blood and tissue samples had already been calculated by Biebach and Keller (2009) with the software PEDANT (Johnson and Haydon 2007).

Identity analyses were performed using CERVUS 3.0 (Kalinowski et al. 2007) and photographs of sampled individuals were used to ensure that multiple samples of single individuals were not mistakenly assigned to different individuals. To increase the quality of the paternity assignments we removed samples of kids without successfully genotyped mothers, and samples that were genotyped at <18 loci. Note that the probability of not being able to distinguish full sibs is <0.001 in the studied population when using samples with ≥18 loci (data not shown). Furthermore, we also excluded males which had never been observed in the study area during the two rutting periods.

Paternity and parameter estimation using MasterBayes

Pedigree reconstruction and the estimation of the parameters of interest were performed simultaneously (i.e. in a so-called full-probability model) in a Bayesian framework using the R package MasterBayes (Version 2.42; Hadfield et al. 2006). MasterBayes provided significant advantages in our case compared to other programs used to infer paternity. First, MasterBayes was able to integrate multiple genotypes of single individuals. Second, it could cope with locus-specific error rates. Third, there was no need to predetermine the proportion of the male population for which genotypes could be obtained. Fourth, the joint estimation of paternity and population-level parameters by MasterBayes was shown to increase the power of paternity assignment, to reduce the bias in parameter estimation, and to evaluate accurately uncertainty in both (for details see Hadfield et al. 2006).

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 (Table 2). Because data on dominance rank and tactic index were not available for all males, we accounted for these missing data by replacing them with 0 (zero) and fitting a secondary binary variable (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 1,000. In 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 we used priors with means of 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 1,000 for continuous or mixed variables (J.D. Hadfield, pers. comm.). The parameters of interest were estimated from the 1,000 MCMC samples from the posterior distribution of the pedigree, and summarised by the median and the range between the quantiles 2.5 and 97.5 (referred to as the 95% credible interval or 95% CI).

Table 2 Population-level parameters estimated from differently parameterized models (1–4) using MasterBayes

Model	Factor	Effect size	Number of 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 assignments at the 80% confidence level
Model 1								
A	A	0.27 (0.20–0.37)	50 and 42	8.6 (1.7–22.7)	0.64 (0.60–0.68)	2.0 (1.7–2.3)	4.8 (4.2–5.7)	8.0
Model 2								
A + A²	A	1.14 (0.55–1.98)	50 and 42	7.9 (1.7–21.6)	0.64 (0.60–0.67)	2.1 (1.8–2.3)	5.0 (4.3–5.7)	7.1
	A²	−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 (4.5–21.7)	0.63 (0.57–0.67)	2.2 (1.9–2.5)	5.6 (4.7–6.7)	7.5
	D	4.26 (2.51–6.10)						
	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 (4.5–24.5)	0.63 (0.57–0.67)	2.1 (1.9–2.5)	5.4 (4.7–6.6)	7.4
	T	2.61 (1.65–3.85)						
	MT	−2.16 (−4.10 to 0.30)						
	A*MT	0.24 (−4.68 to 0.49)						

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, 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

[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)

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 (Shuster and Wade 2003), were both calculated from the 1,000 MCMC samples from the posterior distribution of the pedigree.

Results

Sex-age structure in 2005–2006 and 2006–2007

Census data revealed that the restricted study area during the first rut in 2005–2006 was inhabited by ≤78 animals, with a mean sex ratio of 0.62 males per female (Table 1). During the rut in 2006–2007, when the whole study population was monitored, ≤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).
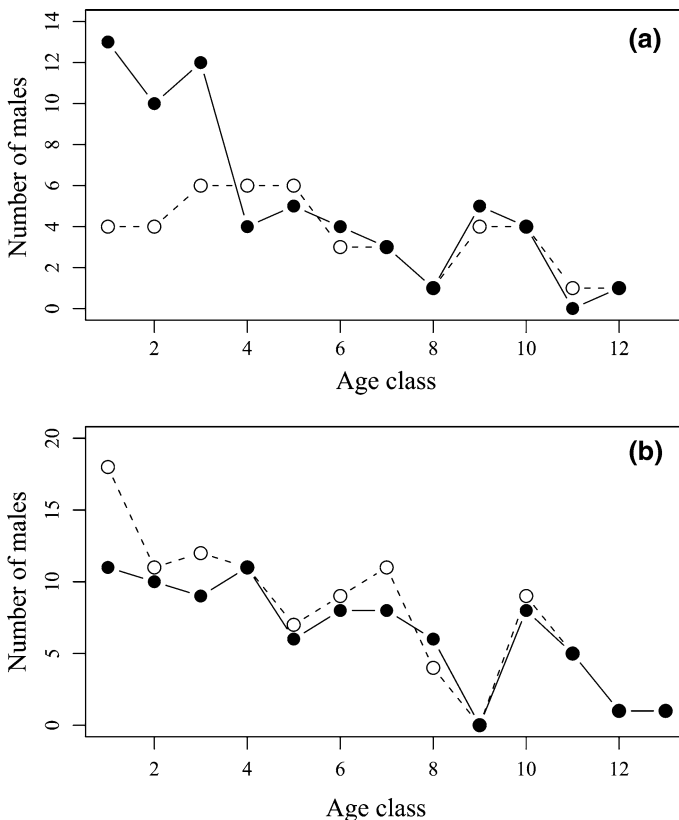

Fig. 1 Maximum number of observed males (*open circles* and *dashed lines*) during daily censuses in the rutting periods of 2005–2006 (**a**) and 2006–2007 (**b**), respectively, and corresponding numbers of males that have been successfully sampled and genotyped (*filled circles* and *solid lines*)

Dominance and mating tactics

During both rutting periods linear dominance hierarchies became apparent (2005–2006: 146 of 253 possible dyads observed, $h' = 0.49$, $P < 0.0001$; 2006–2007: 275 of possible 1,081 dyads observed, $h' = 0.15$, $P = 0.0002$). Individual dominance ranks of males were strongly age-dependent (REML, $n = 64$, $df = 61$, $t = 9.93$, $P < 0.0001$; effect size of age: 0.11 ± 0.01, mean $\pm$ 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, $n = 57$, $df = 54$, $t = 8.85$, $P < 0.0001$; effect size of age: 0.20 ± 0.02, mean $\pm$ SE) with males older than 6–7 years predominately adopting the tending tactic to attain access to receptive females, while younger males of ≤ 5 year of age mainly used the coursing tactic (Fig. 2). Strong positive correlations between dominance ranks and tactic indices existed in both years (2005–2006: $n = 21$, $r = 0.79$, $P < 0.0001$; 2006–2007: $n = 36$, $r = 0.89$, $P < 0.0001$). Tending was the tactic most often used by males with a dominance rank of >0.6, whereas males with lower dominance ranks adopted primarily the coursing tactic.
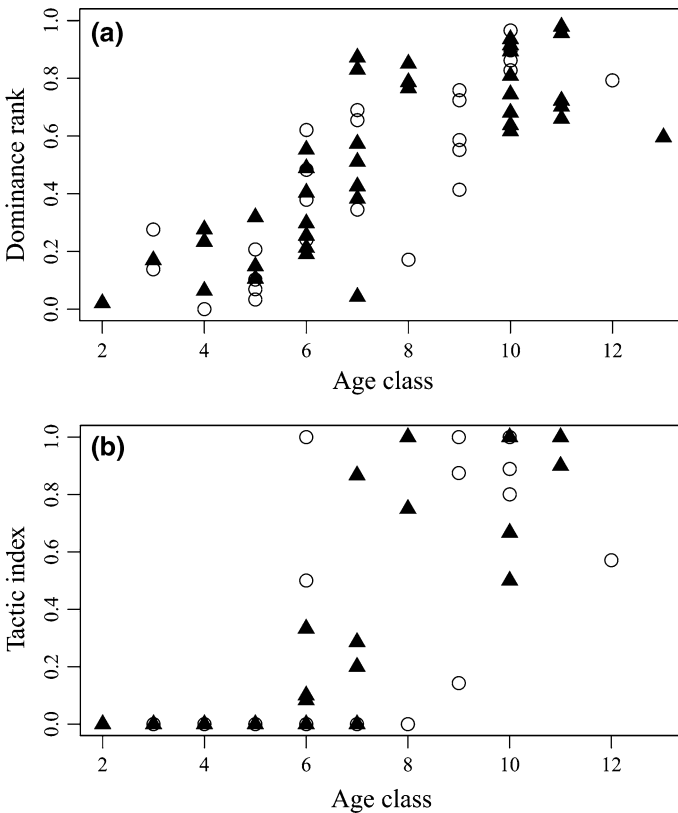

Fig. 2 Relationship between age and dominance rank (**a**) and age and tactic index (**b**) of individual males during the pre-rut and rutting seasons in 2005–2006 (*open circles*) and 2006–2007 (*closed triangles*)

Number of genotyped samples and individuals

In total, 449 DNA samples (369 faecal, 42 blood 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 was 2.88 ± 1.07 (Appendix). For faecal samples, locus-specific rates for allelic dropouts and false alleles per genotype were 5.2 ± 6.9 and 1.6 ± 1.5%, respectively. Because each faecal sample was repeatedly genotyped for ≥3 times, actual error rates of the consensus genotypes are, however, smaller: e.g. the probability of undetected allelic dropout is reduced to 0.03 for the locus with the highest estimated dropout rate (OarHH35). The error rates for blood and tissue samples were estimated by Biebach and Keller (2009) and varied around 1.1 ± 2.2 and 0 ± 0.1%, respectively (Appendix).

After removal of samples that amplified at less than 18 loci and samples of known males that were not observed during the rut, 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. For the paternity tests, 62 and 84 males were considered for the kids born in the 2 years, 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. The number of males that were successfully genotyped corresponded overall well with the number of observed males in the specific age classes (Fig. 1) providing support of the notion that we achieved to sample most of the males present during the two rutting periods. The 13 and 57 kids which 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 differing parameterisation, the four models resulted overall in similar pedigrees. All models made the same assignments to particular kids in 91.4% of all cases at a confidence level of 80%, and in 81.4% at a confidence level of 95%. The 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. 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.

Factors affecting paternity

The two models 1 and 2 containing age and age^2 as factors, demonstrated that the likelihood of siring offspring tended to rise initially with increasing age (Table 2). After the age of 11 years, the likelihood of siring offspring decreased again (Fig. 3). The median individual reproductive success did not increase before the age of 10 years, although variation among 7 and 8 years 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). None of the
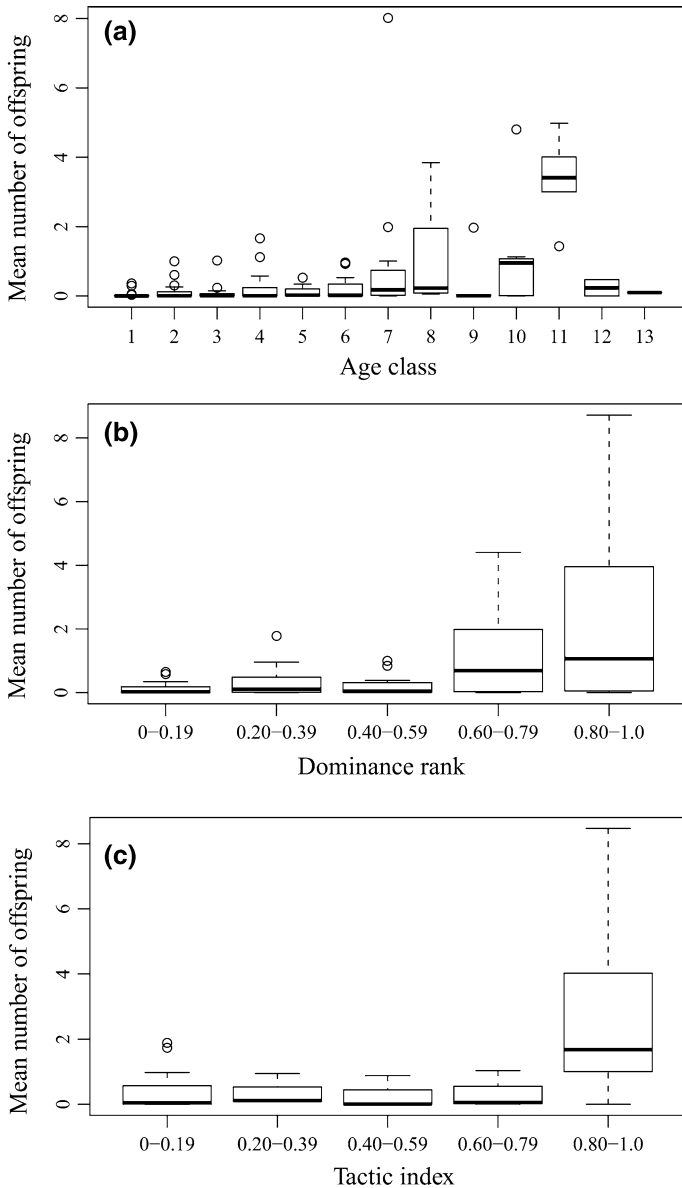
Fig. 3 Box-plots of the mean number of offspring per individual male (offspring cohorts 2006 and 2007 pooled) in relation to the age (**a**), the dominance ranks (**b**) and tactic indices (**c**) of males during the preceding ruts, based on the posterior distribution of the 1,000 MCMC sample pedigrees of model 1, 3 and 4, respectively

12–13 year old animals were assigned ≥1 paternity. However, these age categories contained only 3 individuals in total.

The significant parameter estimates for dominance rank (model 3) and tactic index (model 4) demonstrated that high dominance and the adoption of the tending tactic were important determinants of male reproductive success (Table 2). Hence, the number of sired

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

offspring increased considerably in animals that held dominance ranks above 0.60 and tactic indices above 0.80 (Fig. 3). Lower-ranking males and males adopting less often the tending tactic only occasionally managed to sire offspring. Medians close to zero indicate that the majority of them had no paternities at all.

Further analyses revealed that paternities assigned to males of ≥8 years of age (when they are expected to be fully grown) were mainly due to individuals adopting chiefly the tending tactic (average tactic index: median = 0.92; 95% CI = 0.90–0.95), while assigned paternities among males ≤7 years of age were mainly due to individuals adopting chiefly the coursing tactic (average tactic index: median = 0.14; 95% CI = 0.10–0.25; based on model 3).

Variation in individual reproductive success and opportunity for selection

The average number of paternities assigned to individual males of the offspring cohort in 2007, when a large portion of kids in the whole study population was sampled, varied around 0.63–0.64 kids per male depending on the chosen model, with variances of 2.0–2.2. 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 4 shows that about 60 males produced no offspring during the rut in 2006–2007; about 15 males sired one offspring, and about 10 males sired 2 or more offspring.

Comparisons with other ungulates

Positive effects of age and dominance rank on male reproductive success were also found in other ungulate species with differing survival rates (Table 4). Frequent reproduction via sneaking tactics at an early age was evident in male bighorn sheep (*Ovis candensis*; Hogg and Forbes 1997), and is likely to occur among male Soay sheep (*Ovis aries*, Stevenson et al. 2004; Coltman et al. 1999a). In bighorn sheep males from 2 to 3 years of age onwards reproduce frequently via the coursing tactic (Coltman et al. 2002; Hogg and Forbes 1997),
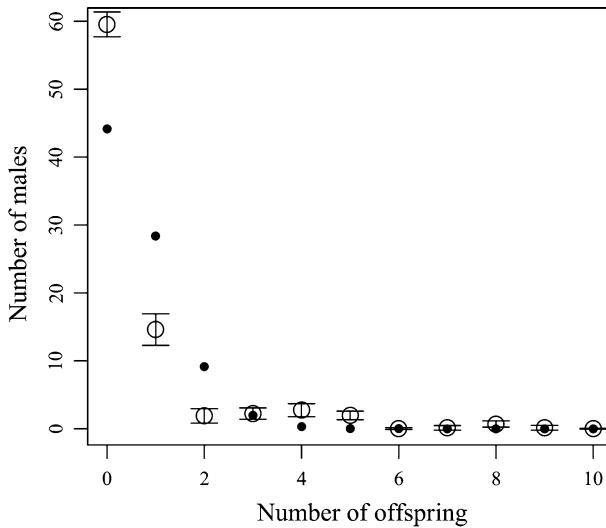
Fig. 4 Observed distribution of assigned paternities (*open circles*; mean ± SD) of the offspring cohort in 2007 among 84 males that were present during the preceding rut and expected distribution of paternities under random assignment (*black dots*), based on the 1,000 MCMC samples of the posterior distribution of the pedigree of model 1

and they were responsible for an average of 44% of all assigned paternities in two populations (Hogg and Forbes 1997). In Soay sheep, the ungulate species with the lowest reported adult survival (Table 4), frequent reproduction was even observed among juvenile males (Coltman et al. 1999a, b), and comparisons of paternity analyses with observations during the rut furthermore suggest that potentially >70% of offspring might have been sired by males adopting a sneaking tactic in this species (Coltman et al. 1999a). In contrast, and similar to Alpine ibex, early reproduction via sneaking appeared to be less important in red deer (*Cervus elaphus*; Pemberton et al. 1992) and wood bison (*Bison bison*; Wilson et al. 2002), two polygynous ungulates with comparatively high adult survival. In these two species, males did seemingly not start to sire a significant number of offspring until the age of 6–7 years (Wilson et al. 2002; Clutton-Brock et al. 1988a; Pemberton et al. 1992).

Overall, reproductive skew in male ungulates showed considerable variation. Apart from Alpine ibex, high values of I_m were also found in fallow deer, bighorn sheep and Soay sheep; moderate values in red deer, roe deer and withe-tailed deer, and low values in wood bison (Table 4).

Discussion

Reproductive pattern of male Alpine ibex

As expected from life-history theory, reproductive success in Alpine ibex was heavily skewed towards older, tending males, while younger males made predominately use of the coursing tactic and sired only few offspring. Age, tactic index and dominance rank, strongly affected the likelihood of individual males siring offspring. On average, highest reproductive success was achieved among (1) males aged 10–11 years, (2) males holding

Table 4 Comparison of different ungulates species with respect to: (1) the average annual survival of adult males (Survival), (2) the effects of age (EA), dominance (ED) and sneaking tactics (ST) on individual male reproductive success, and (3) the reproductive skew (I_m)

Species	Survival	EA	ED	ST	I_m	References
Capra ibex	0.95	+	+	Insignificant	4.8–5.6 (SS)[b] 7.1–8.0 (SS)	This study; Toigo and Gaillard (2003), Toigo et al. (2007)
Bison bison	0.95	+	+	Insignificant	1.2 (MPS) 0.5[c] (AMS)	Toigo and Gaillard (2003), Wilson et al. (2002), Wolff (1998)
Cervus elaphus[a]	0.94	+	+	Insignificant	7.2 (SS) 2.5 (L)	Clutton-Brock et al. (1988a), Appleby (1982), Coltman et al. (2002), Pemberton et al. (1992), Toigo and Gaillard (2003)
Capreolus capreolus	0.87	+	No data	No data	2.5 (MPS) 0.8 (L)	Toigo and Gaillard (2003), Vanpe et al. (2008, 2009)
Rangifer tarandus	0.85	+	+	No data	No data	Roed et al. (2002, 2005), Toigo and Gaillard (2003)
Dama dama[a]	0.83	+	+	No data	5.7[c] (AMS)	Clutton-Brock et al. (1988b), McElligott et al. (2002), McElligott and Hayden (2000);, McElligott et al. (1998), Say et al. (2003)
Ovis Canadensis	0.82	+	+	Important	4.5 (AMS)	Bonenfant et al. (2009), Coltman et al. (2002), Hogg and Forbes (1997)
Odocoileus virginianus	0.74	+	No data	No data	1.9 (SS)	Ricca et al. (2002), Sorin (2004)
Ovis aries	0.68	+	+	Important	4.0 (AMS) 2.6 (L)	Clutton-Brock et al. (1992), Coltman et al. (1999b), Pemberton et al. (1999), Stevenson et al. (2004)

The method of I_m estimation is indicated in brackets (L, estimate is derived from life time breeding success; MPS, estimate is derived from multiple, but pooled seasons; SS, estimate is derived from one single breeding season; AMS, estimate is average from multiple seasons)

[a] In these species calculations of age- and rank-dependent reproductive success and I_m were based on behavioural estimates which reliably reflect the relative reproductive success among males (Pemberton et al. 1992; Say et al. 2003)

[b] Based on the 1000 MCMC samples of the posterior distribution

[c] Only breeding males considered, i.e. males having sired ≥1 offspring

dominance ranks above 0.8, and (3) males adopting the tending tactic in more than 80% of observations. The only exception in this regard was a 7 year old male that was ascribed >8 paternities in the 2006–2007 offspring cohort, which is the highest reproductive success recorded in our study for a single individual. This male was highly dominant and made extensive use of the tending tactic (Figs. 2, 3), suggesting that it was a high quality male above age-specific average (see also Bergeron et al. 2010). Overall, the age of males appears to be only of secondary importance for individual reproductive success, while the factors ultimately determining individual success are a high dominance rank and the adoption of the tending tactic.

Nevertheless, consistent with behavioural observations (Willisch and Neuhaus 2009, 2010) and findings in male bighorn sheep (Hogg and Forbes 1997), the dominance of an individual relative to its competitors was only important among older, fully grown males who gain paternities via the tending tactic, whereas it appeared to provide no immediate advantages to younger, coursing males. This notion is supported by the finding that the 2–4 year old males appeared to be slightly more successful than the distinctly bigger and higher-ranking males of 5–6 years of age (Table 3). In coursing males, agility and running speed rather than dominance are probably the crucial determinants (Willisch and Neuhaus 2009; Hogg and Forbes 1997), since only males that are able to outrun their competitors and catch up with females will have a chance to mate with receptive females during or following a coursing chase.

Although our data do not allow us to infer with certainty the proportional success of the coursing tactic, our data suggest that only about 11% of the offspring have been sired by males adopting this tactic, whereas the remaining 89% appear to be the result of the tending tactic. The minor success of coursing male Alpine ibex stands in sharp contrast with the higher reproductive success of coursing, young, aggressively competing male bighorn sheep (Hogg and Forbes 1997) and Soay sheep (Coltman et al. 1999a, b; Preston et al. 2001). Compared to bighorn sheep and Soay sheep, in which coursing appears to be a high cost—high gain tactic (Hogg and Forbes 1997; Pelletier 2005; Preston et al. 2001), coursing in male Alpine ibex seems to be a rather opportunistic low cost—low gain tactic (Willisch and Neuhaus 2009). This impression is further corroborated by the fact that coursing male Alpine ibex did evidently not make use of overt aggression against the tending male during the rut in order to obtain transient mating access to receptive females (Willisch and Neuhaus 2009, 2010). Considering that the rut of Alpine ibex takes place in very steep and exposed terrain, the risks associated with intra-male aggression and coursing chases might, however, also be much higher than in many other ungulates, contributing to the less aggressive behaviour of Alpine ibex.

Reproductive pattern and survival in other ungulates

Positive effects of age and dominance on reproductive success are not restricted to male Alpine ibex; they can be found in a variety of other polygynous ungulates as well (see e.g. Coltman et al. 1999b, 2002; Nussey et al. 2009). However, in no other species has such a strong age-related reproductive skew towards males of older ages been documented as in the Alpine ibex in our study. This finding is in accordance with the extremely high survival of male Alpine ibex (Toïgo et al. 2007).

Among polygynous ungulates in general, reproduction at an early age appears to be comparably frequent among species with poor to moderate survival prospects, whereas its significance seems to be relatively low in species exhibiting high annual survival rates. Thus, in bighorn sheep, white-tailed deer (*Odocoileus virginianus*), reindeer (*Rangifer*

tarandus), and roe deer (*Capreolus capreolus*)—all species with annual survival rates varying between 74 and 87% on average (Bonenfant et al. 2009; Toigo and Gaillard 2003; Ricca et al. 2002)—successful reproduction is taking place already among 1–4 year old individuals (Sorin 2004; Coltman et al. 2002; Roed et al. 2005; Vanpe et al. 2009). In Soay sheep, a polygynous ungulate whose average annual survival may be as low as 68% (Toigo and Gaillard 2003; Clutton-Brock et al. 1992), frequent reproduction was even observed among juvenile individuals (Coltman et al. 1999a, b). On the other hand, in red deer (Nussey et al. 2009) and wood bison (Wilson et al. 2002)—i.e. two species exhibiting relatively high survival rates of on average 94–95% (Toigo and Gaillard 2003)—reproductive success is largely restricted to males older than 5–7 years.

Data on the distribution of male reproductive success are so far only available for few ungulate species. These data show that male reproductive behaviour in polygynous species is highly plastic (Oliveira et al. 2008; Isvaran 2005). Furthermore, the above compilation of survival and reproduction patterns illustrates that, similar to female mammals (e.g. Dobson and Oli 2007), male ungulates also exhibit a close link between age-dependent reproductive patterns and overall prospects of reaching full adult body size. Thus, as expected from life-history theory, high survival rates coincide with a delayed start of reproduction among polygynous male ungulates, whereas poor survival prospects are associated with early reproduction.

Reproductive skew

Our finding that reproductive success in male Alpine ibex was largely restricted to few older, high ranking males engaging primarily in the tending tactic, led to a marked reproductive skew among males in the population. The values of I_m we found were among the highest reported for polygynous ungulates. Still, contrary to expectations, the level of reproductive skew in the different species was not associated with age-related reproductive patterns of males Table 4). For example, Soay sheep exhibit frequent early reproduction and I_m values nearly as high as Alpine ibex, while wood bison exhibit a delayed onset of reproduction like Alpine ibex but low I_m values. Thus, even in species in which early reproduction is very frequent, the distribution of paternities may still be noticeably restricted to few, but very successful individuals; the opposite may be the case in species with delayed reproduction.

Conclusions

In accordance with existing studies on growth (Lüps et al. 2007) and survival (Toïgo et al. 2007), our study confirmed the prediction that male Alpine ibex are exhibiting a reproductive pattern that is strongly biased towards older males. Therefore, not just with regard to survival but also with regard to reproduction, male Alpine ibex live a rather slow life when compared with other polygynous ungulates. Slow life-histories as described here for male Alpine ibex are thought to evolve only in environments allowing for persistently high yearly survival rates. That male adult Alpine ibex exhibit consistently high adult survival rates on average appears to be a consequence of their excellent ability to buffer the climate-induced environmental variability typical of their harsh alpine habitat (Grotan et al. 2008). Nevertheless, should their survival decrease significantly, male Alpine ibex are expected to experience selection for faster life-history, as evidenced for Tasmanian devils (*Sarcophilus harrisii*) which responded to the occurrence of a deadly disease by becoming increasingly precocious (Jones et al. 2008). To which extent the human-induced hunting pressure in the

history of Alpine ibex (Biebach and Keller 2009) has already led to shifts in the life-history strategy of this species, especially the age-dependent reproductive pattern, remains unknown. Given the large reproductive skew, I_m, and the correspondingly high 'opportunity for selection' (Shuster and Wade 2003), this aspect would doubtlessly merit further analyses, since high values of I_m are indicating that heritable traits in males can react quickly to selection (see also Coltman et al. 2003; Conover and Munch 2002; Harris et al. 2002).

Appendix

See Table 5.

Table 5 Expected heterozygosity (H_e) and locus-specific error rates (per genotype) for faecal and blood/tissue samples

Locus	Number of alleles	Faecal samples		Blood and tissue samples[a]		H_e
		Dropout rate	False allele rate	Dropout rate	False allele rate	
BM1258	5	0.009	0	0	0	0.29
BM1818	2	0.113	0.012	0.026	0	0.50
BM302	4	0.014	0.006	0	0	0.69
BM415	2	0.035	0.031	0	0	0.44
BM4208	4	0.007	0.018	0.009	0	0.74
BM4505	2	0.203	0.033	0.074	0	0.46
CSSM47	3	0.016	0.005	0.071	0	0.53
ETH10b	2	0.058	0.002	0.019	0	0.12
HAUT27	3	0.122	0.029	0.02	0	0.46
ILSTS029	2	0.054	0.061	0	0.005	0.50
INRABERN175	2	0.064	0.038	0.01	0	0.48
JMP29	3	0.01	0.006	0.025	0	0.60
Maf209	3	0	0	0	0	0.10
MAF36	3	0.014	0.01	0	0	0.10
MAF70	2	0.041	0.004	0	0	0.08
McM152	4	0.003	0.004	0	0	0.65
McM73	4	0.011	0.025	0	0	0.69
MILSTS076	5	0.028	0.021	0	0	0.45
OarAE54	2	0.065	0.008	0.071	0	0.23
OARFCB193	6	0.017	0.012	0	0	0.55

Table 5 continued

Locus	Number of alleles	Faecal samples		Blood and tissue samples[a]		H_e
		Dropout rate	False allele rate	Dropout rate	False allele rate	
OARFCB20	2	0.006	0	0	0	0.35
OarFCB48	2	0.02	0.007	0	0	0.40
OarHH35	3	0.318	0.049	0	0	0.56
OarHH62	3	0.126	0.031	0.011	0	0.22
OarkP6	2	0.019	0.007	0	0	0.19
OarVH34	2	0.026	0.006	0	0	0.51
SR-CRSP23	2	0.026	0.022	0	0	0.35
SR-CRSP07	2	0.158	0.004	0	0	0.32
SR-CRSP25	3	0.015	0.018	0.025	0	0.59
TGLA10	3	0.01	0.007	0	0	0.39
TGLA126	3	0.029	0.009	0	0	0.38
URB058	2	0.017	0.018	0	0	0.28
Mean (±SD)	2.88 (1.07)	0.052 (0.069)	0.016 (0.015)	0.011 (0.022)	0.000 (0.001)	0.41 (0.18)

H_e and error rates of blood and tissue samples were calculated using another data set

[a] Published by Biebach and Keller (2009)

References

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

Bell G (1980) The costs of reproduction and their consequences. Am Nat 116(1):45–76

Bergeron P, Grignolio S, Apollonio M, Shipley B, Festa-Bianchet M (2010) Secondary sexual characters signal fighting ability and determine social rank in Alpine ibex (*Capra ibex*). Behav Ecol Sociobiol 64:1299–1307

Biebach I, Keller LF (2009) A strong genetic footprint of the re-introduction history of Alpine ibex (*Capra ibex ibex*). Mol Ecol 18(24):5046–5058

Bonenfant C, Pelletier F, Garel M, Bergeron P (2009) Age-dependent relationship between horn growth and survival in wild sheep. J Anim Ecol 78(1):161–171

Clutton-Brock TH (1984) Reproductive effort and terminal investment in iteroparous animals. Am Nat 123(2):212–229

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

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

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

Clutton-Brock TH, Price OF, Albon SD, Jewell PA (1992) Early development and population fluctuations in Soay sheep. J Anim Ecol 61(2):381–396

Coltman DW, Bancroft DR, Robertson A, Smith JA, Clutton-Brock TH, Pemberton JM (1999a) Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. Mol Ecol 8(7):1199–1209

Coltman DW, Smith JA, Bancroft DR, Pilkington J, MacColl ADC, Clutton-Brock TH, Pemberton JM (1999b) Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. Am Nat 154(6):730–746

Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C (2002) Age-dependent sexual selection in bighorn rams. Proc R Soc Lond Ser B Biol Sci 269(1487):165–172

Coltman DW, O'Donoghue P, Jorgenson JT, Hogg JT, Strobeck C, Festa-Bianchet M (2003) Undesirable evolutionary consequences of trophy hunting. Nature 426(6967):655–658

Conover DO, Munch SB (2002) Sustaining fisheries yields over evolutionary time scales. Science 297(5578):94–96

Coté SD (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. Anim Behav 55:827–843

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

Dobson FS, Oli MK (2007) Fast and slow life histories of mammals. Ecoscience 14(3):292–299

Grotan V, Saether BE, Filli F, Engen S (2008) Effects of climate on population fluctuations of ibex. Glob Change Biol 14(2):218–228

Hadfield JD, Richardson DS, Burke T (2006) Towards unbiased parentage assignment: combining genetic, behavioural and spatial data in a Bayesian framework. Mol Ecol 15(12):3715–3730

Harris RB, Wall WA, Allendorf FW (2002) Genetic consequences of hunting: what do we know and what should we do? Wildl Soc Bull 30(2):634–643

Harvey PH, Zammuto RM (1985) Patterns of mortality and age at 1st reproduction in natural-populations of mammals. Nature 315(6017):319–320

Hogg JT, Forbes SH (1997) Mating in bighorn sheep: frequent male reproduction via a high-risk ''unconventional'' tactic. Behav Ecol Sociobiol 41(1):33–48

Isvaran K (2005) Variation in male mating behaviour within ungulate populations: patterns and processes. Curr Sci 89(7):1192–1199

Johnson PCD, Haydon DT (2007) Maximum-likelihood estimation of allelic dropout and false allele error rates from Microsatellite genotypes in the absence of reference data. Genetics 175(2):827–842

Jones ME, Cockburn A, Hamede R, Hawkins C, Hesterman H, Lachish S, Mann D, McCallum H, Pemberton D (2008) Life-history change in disease-ravaged Tasmanian devil populations. Proc Natl Acad Sci USA 105(29):10023–10027. doi:10.1073/pnas.0711236105

Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol 16(5):1099–1106

Kozlowski J (1992) Optimal allocation of resources to growth and reproduction—implications for age and size at maturity. Trends Ecol Evol 7(1):15–19

Loison A, Gaillard JM, Pelabon C, Yoccoz NG (1999) What factors shape sexual size dimorphism in ungulates? Evol Ecol Res 1(5):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

McElligott AG, Hayden TJ (2000) Lifetime mating success, sexual selection and life-history of fallow bucks (Dama dama). Behav Ecol Sociobiol 48(3):203–210

McElligott AG, Mattiangeli V, Mattiello S, Verga M, Reynolds CA, Hayden TJ (1998) Fighting tactics of fallow bucks (Dama dama, Cervidae): Reducing the risks of serious conflict. Ethology 104(9):789–803

McElligott AG, Altwegg R, Hayden TJ (2002) Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (Dama dama). Proc R Soc Lond Ser B Biol Sci 269(1496):1129–1137

Nussey DH, Kruuk LEB, Morris A, Clements MN, Pemberton JM, Clutton-Brock TH (2009) Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. Am Nat 174(3):342–357

Oliveira RF, Taborsky M, Brockmann HJ (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. Behav Ecol 16(1):280–285

Pemberton JM, Albon SD, Guinness FE, Cluttonbrock TH, Dover GA (1992) Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. Behav Ecol 3(1):66–75

Pemberton JM, Coltman DW, Smith JA, Pilkington JG (1999) Molecular analysis of a promiscuous, fluctuating mating system. Biol J Linnean Soc 68(1–2):289–301

Pianka ER, Parker WS (1975) Age-specific reproductive tactics. Am Nat 109(968):453–464

Preston BT, Stevenson IR, Pemberton JM, Wilson K (2001) Dominant rams lose out by sperm depletion—a waning success in siring counters a ram's high score in competition for ewes. Nature 409(6821): 681–682

Promislow DEL, Harvey PH (1990) Living fast and dying young—a comparative analysis of life-history variation among mammals. J Zool 220:417–437

Ratti P, Habermehl KH (1977) Investigations into age estimation and age determination of mountain ibex (Capra ibex ibex) in Kanton Graubunden. Z Jagdwiss 23(4):188–213

Ricca MA, Anthony RG, Jackson DH, Wolfe SA (2002) Survival of Columbian white-tailed deer in western Oregon. J Wildl Manag 66(4):1255–1266

Roed KH, Holand O, Smith ME, Gjostein H, Kumpula J, Nieminen M (2002) Reproductive success in reindeer males in a herd with varying sex ratio. Mol Ecol 11(7):1239–1243

Roed KH, Holand O, Gjostein H, Hansen H (2005) Variation in male reproductive success in a wild population of reindeer. J Wildl Manag 69(3):1163–1170

Say L, Naulty F, Hayden TJ (2003) Genetic and behavioural estimates of reproductive skew in male fallow deer. Mol Ecol 12(10):2793–2800

Shuster SM, Wade MJ (2003) Mating systems and strategies. Monographs in behavior and ecology. Princeton University Press, Princeton

Sorin AB (2004) Paternity assignment for white-tailed deer (Odocoileus virginianus): mating across age classes and multiple paternity. J Mammal 85(2):356–362

Stearns SC (1976) Life-history tactics—review of ideas. Q Rev Biol 51(1):3–47

Stearns SC (1983) The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. Oikos 41(2):173–187

Stearns SC (1992) The evolution of life histories. Oxford University Press, New York

Stevenson IR, Bancroft DR (1995) Fluctuating trade-offs favour precocial maturity in male Soay sheep. Proc R Soc Lond Ser B Biol Sci 262(1365):267–275

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

Taberlet P, Waits LP, Luikart G (1999) Noninvasive genetic sampling: look before you leap. Trends Ecol Evol 14(8):323–327

Toigo C, Gaillard JM (2003) Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? Oikos 101(2):376–384

Toïgo C, Gaillard JM, Festa-Bianchet M, Largo E, Michallet J, Maillard D (2007) Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. J Anim Ecol 76(4):679–686

Valiere N (2002) GIMLET: a computer program for analysing genetic individual identification data. Mol Ecol Notes 2(3):377–379

Vanpe C, Kjellander P, Galan M, Cosson JF, Aulagnier S, Liberg O, Hewison AJM (2008) Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. Behav Ecol 19(2):309–316

Vanpe C, Gaillard JM, Morellet N, Kjellander P, Liberg O, Delorme D, Hewison AJM (2009) Age-specific variation in male breeding success of a territorial ungulate species, the European roe deer. J Mammal 90(3):661–665

Wehausen JD, Ramey RR, Epps CW (2004) Experiments in DNA extraction and PCR amplification from bighorn sheep feces: the importance of DNA extraction method. J Hered 95(6):503–509

Williams GC (1966) Natural selection costs of reproduction and a refinement of lacks principle. Am Nat 100(916):687–690

Willisch CS, Neuhaus P (2009) Alternative mating tactics and their impact on survival in adult male Alpine ibex (Capra ibex ibex). J Mammal 90(6):1421–1430

Willisch CS, Neuhaus P (2010) Social dominance and conflict reduction in rutting male Alpine ibex, Capra ibex. Behav Ecol 21:372–380

Wilson GA, Olson W, Strobeck C (2002) Reproductive success in wood bison (Bison bison athabascae) established using molecular techniques. Can J Zool Revue Canadienne de Zoologie 80(9):1537–1548

Wolff JO (1998) Breeding strategies, mate choice, and reproductive success in American bison. Oikos 83(3):529–544