



# Preliminary analysis of reproductive success in a large mammal with alternative mating tactics, the Northern chamois, *Rupicapra rupicapra*

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In polygynous mating systems, reproductive skew depends on the ability of males to monopolize females, which in turn may promote the development of contrasting traits in the two sexes. Although dominant individuals normally enjoy a higher reproductive success (RS) than subordinates, the use of genetic markers has shown that behavioural observations of male mating success may not provide reliable clues of RS. We report the preliminary results of the first DNA-based paternity analysis on the Northern chamois (*Rupicapra rupicapra*), a scarcely dimorphic mountain ungulate described as highly polygynous, in relation to mating tactic and age. Because of sampling difficulties, the success in parentage assignment was low, and the interpretation of results requires caution. Territorial males had a greater RS than nonterritorial ones but they were unable to monopolize mating events. Age had a weak effect on paternity outcome but only males  $\geq 6$  years showed siring success. Although future studies are needed to assess the opportunity for sexual selection in male chamois, the concurrence of limited sexual size dimorphism, compensatory growth, unbiased sex-specific survival, RS of alternative mating tactics and, possibly, long breeding tenure, may hint at the adoption of a conservative mating strategy in this species. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, 116, 117–123.

**ADDITIONAL KEYWORDS:** breeding lifespan – mating system – paternity – sexual selection – ungulates.

## INTRODUCTION

Sexual selection, as originally theorized by Darwin (1871), can be described as selection for traits that increase mating success, which rises in response to either male mating competition or female mate choice. The relationship between the intensity of sexual selection and mating systems suggests that the

variation in reproductive success (RS) should be higher in males than females in polygynous species (Clutton-Brock, 1983) as a result of the intense male–male competition, which, in turn, may promote the evolution of contrasting traits in the two sexes, such as body size or weaponry (Andersson, 1994).

In polygynous mating systems, the distribution of paternity depends on the ability of males to secure and fertilize oestrus females. Dominant individuals normally enjoy a higher RS than low-ranking ones,

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for example in relation to hormonal status, age or size (Clutton-Brock, 1988). Over recent decades, the use of genetic markers has shown that behavioural observations of male mating success may not provide reliable clues of RS (Coltman *et al.*, 1999). The skew in male RS, for example, may be less pronounced than expected owing to the difficulty experienced by dominant males in preventing surreptitious matings, which has increasingly drawn attention towards variation in mating behaviour (i.e. alternative mating tactics). In turn, a reduction in the potential to monopolize females is expected to favour longer breeding tenures in males (Lukas & Clutton-Brock, 2014).

In the present study, we report the preliminary results of the first paternity analysis conducted on the Northern chamois (*Rupicapra rupicapra*), a mountain-dwelling ungulate widely distributed in Europe and the near East, earlier described as highly polygynous (Loison *et al.*, 1999). In chamois, the two sexes show several physical minor differences; body mass dimorphism is highly seasonal, possibly the outcome of a conservative male strategy to accumulate fat resources in summer to be used up during the rut (Rughetti & Festa-Bianchet, 2011) and reduce the age- and sex-specific differences in survival (Bocci, Canavese & Lovari, 2010). Because in ungulates the size dimorphism generally increases with the degree of polygyny (Loison *et al.*, 1999), these findings may suggest the adoption of a more conservative mating strategy (i.e. a less intense and less energetically demanding competition among males) compared to that of highly dimorphic species (Garel *et al.*, 2011). A less skewed distribution of paternity, possibly related to the occurrence of alternative mating tactics (i.e. territorial and nonterritorial males; Corlatti *et al.*, 2012), may favour survival and a long male breeding lifespan.

We aimed to investigate the distribution of paternity in chamois in relation to mating tactic (territorial vs. nonterritorial males) and age. We predict that: (1) territorial males should enjoy a higher RS than nonterritorial males, as suggested by behavioural observations (Corlatti *et al.*, 2013), although they are unlikely to monopolize females, and (2) given the rather conservative life history, age should have a weak effect on the paternity outcome in adult individuals.

## MATERIAL AND METHODS

### STUDY AREA AND POPULATION

The 'upper Orco Valley' study site covers an area of 10 km<sup>2</sup> between 1800 and 3000 m a.s.l. within the

Gran Paradiso National Park (GPNP; Western Italian Alps, 45°26' 30" N, 7°08' 30" E). During the study period, the area was characterized by daily mean precipitation rates of between 2.7 mm in winter and 4.5 mm in autumn, and by daily minimum temperatures averaging between -7.8 °C in winter and 7.3 °C in summer (own data). The valley is oriented west to east, with a south-facing slope dominated by meadows of coloured fescue *Festuca varia*, and a north-facing slope characterized by woods of larch *Larix decidua* and patches of alder shrubs *Alnus viridis*. The chamois population in the GPNP has been protected since 1922 and the adult male population size in the study site, estimated through mark-resight in 2013, was 93 individuals (confidence interval = 63–137) (Corlatti, Fattorini & Nelli, 2015). GPNP counts reported the presence of, at least, 28 offspring in 2011, and 22 in both 2012 and 2013.

Between 2010 and 2012, 36 adult chamois (29 males and seven females) were darted by the Park personnel: we estimated their age (in years) by counting horn rings (Schröder & von Elsner-Schack, 1985) and we also collected tissue samples. Each animal was equipped with an individually recognizable Global Positioning System (GPS) collar: GPS data confirmed that all males remained in the study area during the rutting seasons. Adult male chamois were classified into territorial ( $N = 11$ ) and nonterritorial ( $N = 18$ ) (Corlatti *et al.*, 2012).

### SAMPLE COLLECTION

For genotyping of chamois, we used a combination of tissue (29 adult males and seven adult females) and faecal samples (30 adult females and 93 offspring) collected over 3 years. Tissue samples were collected during captures through gristle ear piercing and immediately stored into tubes with 96% ethanol and preserved at -20 °C until analysis. Faecal sampling was carried out in October of 2011, 2012, and 2013: each year, over two consecutive days, six operators walked the entire study area searching for groups of female chamois with offspring. To reduce double sampling, three groups of two people surveyed different areas simultaneously and the same areas were never surveyed twice. When a group of chamois was spotted, we observed offspring until defecation and faeces were collected soon afterward to avoid degradation. When possible, we collected faecal samples of the corresponding mothers. Faecal samples were immediately stored into plastic boxes with silica gel and kept at room temperature until analysis. In 2011, 2012, and 2013, we collected, respectively, 28, 32, and 33 samples from offspring and five, 15, and 10 samples from mothers.

## DNA EXTRACTION AND PATERNITY ANALYSIS

DNA from tissue samples was extracted using DNeasy Blood & Tissue Kit (Qiagen) in accordance with the manufacturer's instructions, whereas DNA from faecal samples was extracted using the QIAamp DNA Stool Mini Kit (Qiagen) in accordance with the manufacturer's instructions with prolonged washing of the pellet surface in the ASL buffer (Qiagen) to 45 min.

Parentage analysis was conducted using 17 microsatellite loci (Zemanová *et al.*, 2015): OarFCB 20, OarFCB 304, SRCRSP05, SY84, CSSM66, ETH10, SY434, INRA121, SRCRSP11, TGLA53, SY259, BOBT24A, BM1258, SRCRSP09, ETH225, ILSTS030, MAF214. Details about primers, polymerase chain reaction (PCR) amplification conditions, fragment detection, and analysis are given in Zemanová *et al.* (2011). For the analysis of microsatellites, at least two positive PCR repetitions were genotyped for each tissue sample. Tissue and faecal samples were analyzed at least three and four times, respectively, to obtain a reliable consensus genotype (Taberlet *et al.*, 1996). Approximately 4% of faecal samples were excluded from analyses as a result of a low amplification success rate (i.e. the consensus genotype could not be established after five PCR repetitions).

The loci used for parentage analyses were sufficiently variable (two to 13 alleles per locus; median = 6), had high heterozygosities for particular loci within adult individuals ( $H_E = 0.037\text{--}0.891$ ; median  $H_E = 0.716$ ), and each adult individual possessed a unique genotype. The mean probabilities of excluding a single randomly chosen unrelated individual from being a parent were calculated for all 17 loci using CERVUS, version 3.0 (Kalinowski, Taper & Marshall, 2007). These analyses were conducted separately for each year (2011–2012–2013) on all adult individuals genotyped in the course of the study. The total exclusionary power exceeded 99.9% in all cases.

Genotypes of kids were first compared with the genotypes of known mothers. The offspring's alleles were subsequently compared with the alleles of the putative parents. In both cases, we used strict criteria when attempting to identify the mother and the father (no mismatches between kid and their parents). If no female and male matched a particular kid at all loci, the sire was categorized as unknown. The results were confirmed using ML-RELATE (Kalinowski, Wagner & Taper, 2006).

## STATISTICAL ANALYSIS

For the years 2010, 2011, and 2012, data on mating tactic (T, territorial; NT, nonterritorial), age at rut (i.e. November, in years), and number of detected

offspring sired each year were available for 29 genotyped males. Twenty-four of them were recorded for the whole 3-year period, whereas five males were recorded for shorter periods, for a total of 80 observations (Table 1). Data from the same males were clearly dependent.

First, data dependence was bypassed by focusing on the 24 males with full data records: we pooled ages by their 3-years means and offspring sired by considering their RS as 'YES' or 'NO' based on the presence, or not, of at least one offspring sired over the 3 years. Thus, each of the 24 individuals was considered only once in our analyses. Chi-squared tests using the function 'p-chisq' were employed to assess the influence of mating tactic and mean age

**Table 1.** ID, mating tactic (T, territorial; NT, nonterritorial), age at November 2010 (in years), and number of detected offspring sired each year, for the 29 genotyped males available between 2010 and 2012 in the study area within the Gran Paradiso National Park.

ID	Mating tactic	Age at November 2010	Offspring sired		
			2010	2011	2012
M1	T	5.5	0	0	
M3	NT	12.5	0		
M4	T	7.5	1	0	0
M5	T	6.5	0	0	0
M7	NT	6.5	1	0	0
M8	NT	5.5	0	0	0
M9	NT	11.5	1	0	
M11	T	7.5	1	3	0
M12	NT	3.5	0	0	0
M13	T	4.5	0	0	3
M14	T	8.5	0	0	0
M15	NT	6.5	0	0	0
M16	T	6.5	1	0	0
M17	T	6.5	1	0	0
M18	NT	7.5	0	0	0
M20	NT	5.5	0		
M21	NT	7.5	0	0	0
M22	NT	4.5	0	0	1
M23	NT	12.5	0	0	
M24	NT	5.5	0	0	0
M25	T	5.5	0	0	0
M26	NT	3.5	0	0	0
M27	NT	11.5	0	0	0
M28	NT	2.5	0	0	0
M29	NT	9.5	0	0	0
M30	NT	7.5	0	0	0
M31	T	6.5	0	0	0
M32	NT	6.5	0	0	0
M33	T	8.5	0	1	0

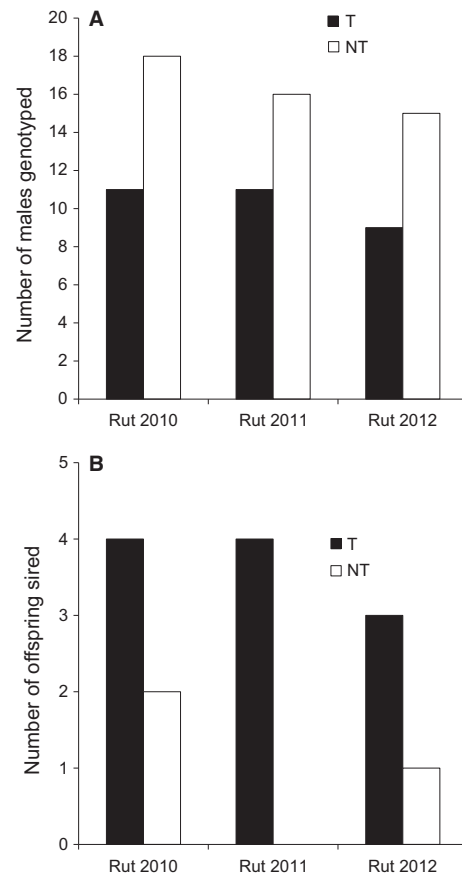
on RS. Furthermore, a logistic regression using the 'glm' function was adopted. The logit transformation of RS probability was presumed to be a linear function of mating tactic and mean age.

On the other hand, if the whole set of 80 observations was used, each individual showed up several times in the analyses and we fitted generalized linear mixed models (GLMM) with a random component addressing for individual effects. As is customary with count data, a Poisson distribution was assumed for the number of sired offspring and was assessed by a chi-squared goodness-of-fit test, using the function 'goodfit'. If a significant presence of zeros was detected, a zero-inflated Poisson mixed model (ZIPMM) was adopted, in which a logistic (or probit) regression was involved for the probabilities of non-zero responses plus a Poisson regression for the probabilities of both zero and non-zero counts (Hall, 2000). ZIPMM was fitted using the function 'glmmadmb'. The log of the expected number of offspring sired was presumed to be a linear function of mating tactic and age plus a random individual effect. All analyses were performed in R, version 3.1.1 (R Development Core Team, 2014).

## RESULTS

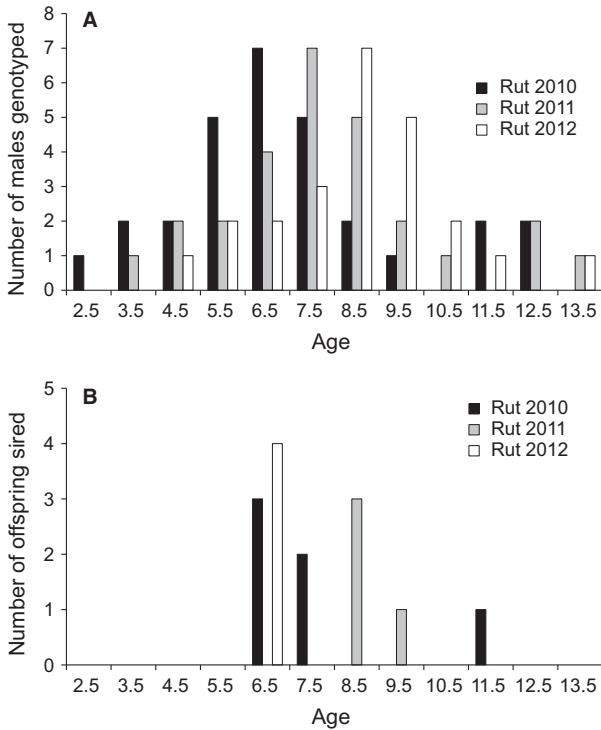
No genotype of adult females, from faeces, was resampled throughout our study. Regarding the genotypes of kids, after accounting for amplification failure, 86 offspring out of 93 samples could be recognized individually. Some kids, however, were sampled more than once within each season, and only 75 offspring were included in parentage analyses, representing approximately 70–80% of the estimated kid population over the 3 years. Thirty of them were assigned to a mother, 26 to a father, and 14 to both parents. Only the latter were used in the statistical analyses: the success in parentage assignment was thus low (19%; i.e. 14 kids out of 75), mainly as a result of difficulties in sampling adult male chamois (approximately 30% of the estimated male population size was sampled).

Figures 1 and 2 show the number of genotyped males available in each year, and their siring success during the ruts of 2010–2011–2012, in relation to mating tactic and age. Table 2 reports the frequency tables for the chi-squared tests performed to assess the influence of mating tactic and mean age, grouped into three classes (< 6.5, 6.5–8.5, > 8.5), on RS. Although mating tactic affected RS (permutation  $P = 0.01$ ), with a 'NO' frequency 3.25 times greater in NT than in T males, mean age was not significant (permutation  $P = 0.89$ ). These results were confirmed by the logistic regression performed on the 24



**Figure 1.** Number of (A) genotyped male chamois and (B) offspring sired, in relation to mating tactic [territorial (T) vs. nonterritorial (NT)] during the ruts of 2010–2011–2012 in the study area within the Gran Paradiso National Park. (A) Twenty-four males show up every year, three males show up in 2010–2011, and two males show up in 2010 only (Table 1).

individuals recorded for the entire study period: only mating tactic had a significant effect ( $\beta = 2.79 \pm 1.15$ ,  $P = 0.02$ ), whereas age had no effect ( $\beta = -0.20 \pm 0.323$ ,  $P = 0.53$ ). When excluding mean age from the model, mating tactic was significant ( $\beta = 2.57 \pm 1.04$ ,  $P = 0.01$ ) and the model predicted a RS probability of 0.67 for T males against 0.13 for NT males. With respect to GLMM, the chi-squared goodness-of-fit test rejected the Poisson distribution ( $P < 0.001$ ) with 57 zeros predicted against 70 observed. Thus, a ZIPMM was adopted to fit the number of sired offspring. The fitting performed on the entire set of 80 individuals confirmed the previous results: only mating tactic had a significant effect ( $\beta = 1.73 \pm 0.72$ ,  $P = 0.02$ ), whereas age had no effect ( $\beta = 0.00 \pm 0.18$ ,  $P = 0.99$ ); if age was discarded, mating tactic was significant ( $\beta = 1.73 \pm 0.71$ ,  $P = 0.02$ ).



**Figure 2.** Number of (A) genotyped male chamois and (B) offspring sired, in relation to age (in years), during the ruts of 2010–2011–2012 in the study area within the Gran Paradiso National Park. (A) Twenty-four males show up every year, three males show up in 2010–2011, and two males show up in 2010 only (Table 1).

**Table 2.** Frequency tables of chi-squared tests performed to assess the influence of mating tactic (T, territorial; NT, nonterritorial) and mean age at rut (in years) on the occurrence of reproductive success (‘YES’ or ‘NO’) in the 24 males within the study area of the Gran Paradiso National Park, for which a full 3-years data record was available

	Reproductive success		Total
	YES	NO	
Mating tactic			
T	6 (3)	3 (6)	9
NT	2 (5)	13 (10)	15
Total	8	16	24
Mean age			
< 6.5	2 (1.67)	3 (3.33)	5
6.5–8.5	5 (5)	10 (10)	15
> 8.5	1 (1.33)	3 (2.67)	4
Total	8	16	24

Values in parenthesis represent expected frequencies.

DISCUSSION

Territorial male chamois had a greater RS than non-territorial ones but were unable to monopolize mating events and, although age had a weak effect on the paternity outcome in sexually mature individuals, only males  $\geq 6$  years showed siring success. These results must be interpreted with some caution, given the practical difficulties involved in genotyping a large proportion of adult individuals. Although the effect of territoriality is confirmed by the statistical analyses, and the GPS data suggest that, over the rut, nonterritorial males stably occupy the study area (L. Corlatti & S. Lovari, unpubl. data), our population cannot be considered isolated. Therefore, we cannot rule out the possibility that potential nonterritorial fathers intruded from neighbour areas. Similarly, the effect of age requires confirmation because of the prevalence of prime-aged males (5–9 years: Stringham & Bubenik, 1975). A sampling design with an even repartition of ages among individuals would be desirable.

Behavioural observations showed that territorial males had greater mating opportunities than nonterritorial males and also monopolized mating events (Corlatti *et al.*, 2013). Although paternity data support the reproductive advantage previously suggested for territorial males (von Hardenberg *et al.*, 2000; Corlatti *et al.*, 2013), they reveal that territorial individuals were unable to prevent surreptitious matings by nonterritorials, thus confirming the importance of using genetic markers to assess the reliability of behavioural observations (Coltman *et al.*, 1999). It remains unclear whether such an advantage is consistent throughout the years or is altered by environmental variability (e.g. snow cover; Lovari, Sacconi & Trivellini, 2006) or by differential trade-offs between mating tactics (Corlatti *et al.*, 2012), although the occurrence of RS in alternative male types possibly suggests a reduction in the skew of paternity outcome (Rubenstein & Nuñez, 2009).

Because male chamois have no need to develop a conspicuous body mass and weaponry (Bassano, Perrone & von Hardenberg, 2003), they may allocate energy reserves to a faster growth and thus to an earlier reproduction, compared to species with slower life histories [e.g. Alpine ibex (*Capra ibex*); Willisch *et al.*, 2012]. This, together with a high survival probability until late age, suggests a long breeding lifespan. The possibly weak effect of age on the paternity outcome observed in the present study suggests that male reproductive tenure may extend well beyond the prime period: it remains unclear whether males  $< 6$  years of age may enjoy RS in protected populations, although Locati & Lovari (1988) showed that males  $\geq 6$  years monopolized mating events,

until at least 13–14 years of age, for the Apennine chamois (*Rupicapra pyrenaica ornata*). This suggests that male chamois may enjoy a prolonged breeding tenure, which may suggest a reduced potential to monopolize females (Lukas & Clutton-Brock, 2014).

Our data do not allow an assessment of the opportunity for sexual selection, and hence the relative level of polygyny in male chamois. As a result of sampling difficulties, we cannot rule out the possibility that one or several unsampled males may have had a high siring success, thus increasing paternity skew. Although in ungulates, the level of polygyny is positively related, to a large extent, to sexual size dimorphism (Loison *et al.*, 1999), this relationship remains poor in many species (Lukas & Clutton-Brock, 2014). Thus, it would be fairly simplistic to assume a low opportunity for sexual selection in chamois solely on the ground of its limited sexual dimorphism. The competitive ability of individuals may be related to different traits in different species, thus promoting selection pressure on particular traits and possibly resulting in a weak sexual size dimorphism (Clutton-Brock, 2007). In chamois for example, territorial and nonterritorial males do not show differences in body and horn size (Corlatti *et al.*, 2012), and agility rather than conspicuous body mass or weaponry size may enhance male mating success (Rughetti & Festa-Bianchet, 2010). Moreover, studies on selection pressures operating in females may also account for weak phenotypical differences between sexes (Clutton-Brock, 2007).

Nevertheless, a growing amount of evidence suggests that the pressure of sexual selection in male chamois may be lower than in highly polygynous species such as red deer or bighorn rams (Vanpé *et al.*, 2008). Indeed, the concurrence of limited sexual dimorphism, compensatory growth (Rughetti & Festa-Bianchet, 2010), high and unbiased sex-specific survival rates, RS of alternative mating tactics and, possibly, the weak effect of age on paternity outcome in adult chamois suggests the adoption of a conservative male mating strategy to maximize survival.

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