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Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate

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In mammals, species with high sexual size dimorphism tend to have highly polygynous mating systems associated with high variance in male lifetime reproductive success (LRS), leading to a high opportunity for sexual selection. However, little information is available for species with weak sexual size dimorphism. In a long-term study population, we used parentage analysis based on 21 microsatellite markers to describe, for the first time, variance in male lifetime breeding success (LBS) of roe deer, a territorial ungulate where males weigh less than 10% more than females. LBS ranged from 0 to 14 (mean = 4.54, variance = 15.5), and its distribution was highly skewed, with only a few males obtaining high LBS and many males failing to breed or siring only one fawn. As predicted for polygynous species with low sexual size dimorphism, the standardized variance in male LBS was low ($I_m = 0.75$) and was only slightly higher than the standardized variance in female LRS ($I_f = 0.53$), suggesting a low opportunity for sexual selection. The I_m value reported here for roe deer is much lower than values reported for highly dimorphic ungulates such as red deer ($I_m > 3$). We suggest that, along a continuum of opportunity for sexual selection, roe deer occupy a position closer to monogamous and monomorphic territorial ungulates than to highly polygynous, sexually dimorphic ungulates with dominance rank–based mating systems such as harems or roving mating systems. *Key words: Capreolus capreolus*, lifetime reproductive success, microsatellite, paternity analysis, roe deer, ungulates. *[Behav Ecol 19:309–316 (2008)]*

Measuring the opportunity for sexual selection is crucial for addressing many questions in behavioral ecology (such as the evolution of sexual size dimorphism, conspicuous male traits, alternative mating tactics, and sex-biased parental investment; Andersson 1994) and population dynamics (such as effective population size; Begon 1984). Sexual selection theory predicts that the opportunity for sexual selection is strong when reproductive success varies widely among males, with a few males highly successful at mating and many others males failing to mate or siring only one (or a few) offspring (Darwin 1871). This has led to the general expectation of an association between strong sexual selection, high mating polygyny, and high variance in male reproductive success (Huxley 1938; Wade 1979; Andersson 1994). Several authors have thus proposed the use of variance in male reproductive success as a measure of the opportunity for sexual selection (e.g., Wade and Arnold 1980; Arnold and Wade 1984; Payne 1984).

The evolution of male-biased sexual size dimorphism is thought to have evolved principally as the result of intrasexual competition over mates, given the scenario of high variance in male reproductive success (Darwin 1871; Andersson 1994). In mammals, the level of sexual size dimorphism is linked to the level of polygyny (e.g., for a review, Alexander et al. 1979; in ungulates: Loison et al. 1999). As a rule, highly dimorphic species are highly polygynous, resulting in high variance in male mating success in a wide range of taxa, including primates (e.g., Clutton-Brock et al. 1977), pinnipeds (e.g., in elephant seal *Mirounga angustirostris* [Gill 1866]: LeBoeuf and Reiter 1988), and ungulates (e.g., in red deer *Cervus elaphus* [Linnaeus 1758]: Clutton-Brock et al. 1988).

However, the general pattern relating variation in male reproductive success, sexual size dimorphism, and level of polygyny in mammals remains unclear for several reasons. First, attempts to estimate variance in male reproductive success have traditionally relied on short-term data and behavioral observations of the number of copulations or the number of social associations during which a male may have exclusive access to a female (see Clutton-Brock 1988). But, because intense competition between males typically restricts effective reproductive activity to a few years of their total adult life span, short-term data may grossly overestimate variation in lifetime reproductive success (LRS) (Clutton-Brock 1988). Second, the recent development of molecular biology tools has revealed some discrepancies between behavioral and genetic estimates of male reproductive success (e.g., Amos et al. 1993; Coltman et al. 1999), mainly due to extrapair copulations in socially monogamous species (e.g., Goossens et al. 1998) and to "sneaky" mating tactics of subordinate males in polygynous species (e.g., Coltman et al. 1999). One important consequence of this is that although variance in male reproductive success may be higher than expected in monogamous monomorphic species, it may be lower than expected in polygynous dimorphic species (Andersson 1994). Finally, the available information on variance in male LRS in mammals is limited to a few studies and concerns almost exclusively highly polygynous and dimorphic species (e.g., in red

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deer: Pemberton et al. 1992; Marshall 1998; bighorn sheep *Ovis canadensis* [Shaw 1804]: Coltman et al. 2002; Soay sheep *Ovis aries* [Linnaeus 1758]: Coltman et al. 1999; Pemberton et al. 1999; but see data for the weakly dimorphic harbor seal *Phoca vitulina* [Linnaeus 1758]: Coltman et al. 1998). This precludes any meta-analysis to detect general patterns in the opportunity for sexual selection among mammals, which would be very useful to better understand the evolution of mating systems (Andersson 1994).

The aim of this study was therefore to provide the first genetic estimate of variance in male lifetime breeding success (LBS) and the opportunity for sexual selection in an ungulate with low sexual size dimorphism, the European roe deer *Capreolus capreolus* (Linnaeus 1758). For this, we used microsatellite and paternity analysis in a long-term monitored population in Sweden. Roe deer males weigh less than 10% more than females (Andersen et al. 1998), defend spatially stable territories, usually from 3 years of age (Hewison et al. 1998), and party size is supposed to be low (generally <5; Liberg et al. 1998). Hence, we predicted that the standardized variance in male breeding success would be much lower in roe deer compared with ungulate species with more pronounced sexual size dimorphism.

MATERIALS AND METHODS

Study species

The European roe deer is a small-sized cervid (adults weigh about 20–30 kg). Females are nonterritorial. During the rutting period, they live solitarily, or with fawns, in overlapping home ranges (Bramley 1970). Although female roe deer are monestrous, 98% of adult females in a population are generally fertilized (Hewison 1996; Hewison and Gaillard 2001). Females normally give birth for the first time at 2 years of age (3–4 years in poor habitats and/or at high density; Gaillard et al. 1992), and thereafter every year, to 1–3 neonates (most commonly twins) in May–June (Gaillard, Liberg, et al. 1998). Males become sexually mature as yearlings but usually do not defend territories before 3 years of age (4 years at high density; Strandgaard 1972; Vincent et al. 1995). The territorial period runs from early spring (in March–April) until late August–early September, encompassing the rut that takes place from mid-July to mid-August (Bramley 1970). The spatial system of the 2 sexes is independent, and male territories can include all, or part of, the home ranges of several females (generally 1–5, but up to 10; Bramley 1970; Strandgaard 1972).

Study site and data collection

The study area was situated at Bogesund (59°23′N, 18°15′E), a mainland peninsula surrounded by water on all sides except to the north, situated on the coast of the Baltic Sea on the inner portion of the Stockholm Archipelago, within the hemiboreal zone in East–Central Sweden. The habitat is fragmented, with approximately 65% forest, 25% fields, and 10% bedrock and bogs. The climate is mild, characterized by moderate winters, with snow cover usually from late December to early March, and relatively warm and dry summers (Kjellander et al. 2006). The only natural predator of roe deer fawns is the red fox *Vulpes vulpes* (Linnaeus 1758). The 2600-ha roe deer research area constituted the major part of the Bogesund peninsula, divided into a 1250-ha western experimental area where hunting was controlled and a 1350-ha eastern control area where hunting continued normally (see Kjellander 2000 for more details).

The present work was carried out in the western part where the roe deer population has been monitored intensively since 1988 by an annual capture–mark–recapture (CMR) procedure (Kjellander et al. 2006). From 1988 onward, roe deer (including 8-month-old fawns) were caught each winter in box traps, sexed, and individually marked with plastic ear tags. In addition, from 1997 onward, neonates were caught by hand every spring (May–June), sexed, and marked with small metallic numbered ear tags. Fawns were thus marked either during their first winter (all caught fawns before 1997 and almost half of the caught fawns from 1997 onward; $N = 379$) or right after birth (half of the caught fawns from 1997 onward; $N = 228$). Mother–offspring relationships were elucidated by direct observation of fawns with their mothers immediately after birth or during autumn (after the summer rut ends, roe deer fawns continue to associate with their mother; Linnell et al. 1998), for the fawns caught immediately after birth. The year of birth of individual animals was either known definitively (animals first caught as newborn fawns or juveniles <1 year old) or estimated from tooth eruption and wear (Cederlund et al. 1992) examined during capture or after death (see below for how potential error in age estimation from tooth wear was handled in the analysis).

Tissue sampling, DNA extraction, and microsatellite genotyping

We collected tissue samples for DNA genotyping from individuals caught for the first time and from unmarked shot roe deer. We usually removed a small (approximately 2×2 mm) piece of ear skin tissue using sheep ear-notching pliers. However, samples taken on newborn fawns from 1997 to 2003 were hair samples ($N = 146$). We sampled, in total, 605 fawns born from 1988 to 2005 (of which 267 had a known mother), 231 candidate fathers, and 352 candidate mothers (see supplementary material 1). Notice that sampled fawns from a given cohort can become candidate parents for later fawn cohorts provided that they survive to sexual maturity and that candidate fathers and mothers can be potential parents for several successive fawn cohorts.

Genotyping was carried out using 22 microsatellite markers (see supplementary material 2) initially isolated from other ungulate species (Galan et al. 2003; Vial et al. 2003), except for Roe5, Roe6, Roe8, and Roe9 isolated specifically from roe deer (Fickel and Reinsch 2000). These 22 microsatellites were divided into 2 multiplex kits of 11 microsatellites each (Galan M, Vanpé C, Cosson JF, Kjellander P, Hewison AJM, unpublished data). DNA extraction from skin biopsy samples was carried out either using DNeasy 96 Tissue Kit (Qiagen, Valencia, CA) or PUREGENE DNA Purification Kit (Gentra systems, Inc, Minneapolis, MN). DNA extraction from hair samples was performed using the Chelex 100 resin method (Biorad, Hercules, CA) as described by Walsh et al. (1991) in a room dedicated to processing rare DNA. For each individual, we extracted a minimum of 10 hair follicles with visible roots, as recommended by Goossens et al. (1998) for a single-tube approach. We amplified microsatellites using the polymerase chain reaction (PCR). For skin samples, the procedure is described in Galan et al. (2003). For hair samples, we used the multiple-tube approach, as recommended by Navidi et al. (1992) and Taberlet et al. (1996) for low-DNA samples, with 3 replications of DNA amplification and genotyping per extraction (preliminary tests comparing genotypes from skin vs. hair samples of the same individual indicated that 3 repetitions were required to determine a consensus genotype that matched the correct genotype). Amplification was performed separately for each of the 22 microsatellites with the same PCR conditions. The samples were run on a monocapillary genotyper ABI PRISM 310 DNA (Applied Biosystems, Foster city, CA). GENESCAN 3.1 and GENOTYPER 2.5 softwares (Applied Biosystems)

were used to size alleles based on a size standard and to score microsatellites on autoradiographs.

Tests of microsatellite markers

Prior to paternity analyses, we checked for Hardy–Weinberg equilibrium, for each locus separately and globally, with exact tests using GENEPOP 3.4 (Raymond and Rousset 1995) and the Markov chain method (10,000 dememorizations, 100 batches, and 5000 iterations per batch). The linkage disequilibrium between pairs of loci was tested with GENEPOP by computing Fisher's Exact test for each contingency table of allele frequencies for all pairs of loci using a Markov chain (10,000 dememorizations, 100 batches, and 5000 iterations per batch). As performing multiple tests tends to increase type I errors, we implemented the false discovery rate (Bejamini and Hochberg 1995; Storey 2002), using the GeneTS package in the R 2.2.1. software. This approach offers an easily interpretable way to control for the proportion of significant results that are in fact type I errors, while simultaneously ensuring that type II errors remain low (no loss of power). The above tests were performed on a subset of the whole sample, that is, individuals born in 1992, in order to reduce multigenerational effects. Allelic frequencies and paternity exclusion probabilities were estimated with CERVUS 2.0 (Marshall et al. 1998) over the whole sample set. CERVUS was also used to determine the observed and expected heterozygosity and the null allele frequency for each locus and across all loci. We evaluated available power for distinguishing between individuals using the program GIMLET (Valière 2002), which determines the probability of identity (i.e., the probability that 2 randomly selected genotypes match by chance; Paetkau and Stroberg 1994), for each locus and across all loci. We also calculated the probability that 2 siblings drawn at random from the population would have identical multilocus genotypes (Waits et al. 2001) for each locus and across all loci.

Paternity assignment

Parentage was assessed using a likelihood-based approach with the program CERVUS 2.0 (Marshall et al. 1998). For each parent–offspring pair, the program calculates a logarithm of odds (LOD) score (logarithm of the likelihood ratio). This score is the likelihood of maternity and paternity of a particular candidate parent relative to an arbitrary individual. Using allele frequency data from the population, the program runs a simulation to estimate the critical difference in LOD score between the most likely and next most likely candidate parent (δ) necessary for assignment at greater than 95% or 80% confidence levels. The simulation incorporates user-defined input parameters such as the total number of candidate parents, the proportion of these parents that have been sampled, the frequency of gaps, and the genotyping error rate (i.e., proportion of loci typed incorrectly, averaged across loci and individuals) in the genetic data. The observed rate of missing data was estimated across all typed samples by the allele frequency module of CERVUS and set at 98.7% of loci typed. From independent repeat genotyping of 294 samples at 21 microsatellite loci, we observed that the typing error rate for our data set was 3.81% per locus (Vanpé C, Galan M, Cosson JF, Kjellander P, Hewison AJM, unpublished data). However, because these repeats were not a random sample of the genotype data (they concerned samples for which the full genotype could not be established from the first run), this error rate is certainly an overestimate. In addition, SanCristobal and Chevalet (1997) have shown that with CERVUS, as long as the error rate is fixed to a value greater than zero, the choice of error rate does not have a major impact on confidence or success rate. We therefore decided to fix the error rate to 1%.

Based on long-term CMR and hunting databases and yearly field observations of animals, we listed the candidate fathers and mothers for each cohort of fawns. Both males and females were considered to be candidate parents for a given fawn cohort if they were defined as alive and potentially reproductive in the previous rut. The last potential participation in the rut for an individual was defined in relation to the moment it was either found dead or last recorded alive. The first potential participation in the rut was set at 1 year old for females and 2 years old for males as a function of the age of sexual maturity in roe deer. When the age of a candidate parent was estimated from tooth wear ($N = 269$ females and 162 males), the first year of potential participation in the rut was backdated by 1 year in order to take into account potential error in the estimation of age (Hewison et al. 1999). The inclusion of candidate parents for which age was estimated should not have a great impact on our results because we did not analyze the age dependence of male breeding success. However, note that if some immature males are erroneously considered as candidate fathers in a given year due to inaccurate age estimation, the number of unsuccessful breeding males may be somewhat overestimated. For this reason, we did not include estimated age males in our analyses of yearly breeding success (YBS), and in our analyses of LBS, we compared the results with and without estimated age males. The proportion of known candidate parents sampled varied among cohorts but was always higher than 80% for fathers and 76% for mothers. In order to take into account potential unknown candidate parents in the population, we decided to fix the proportion of candidate parents sampled to a conservative value of 75% for all years and for both sexes. The total number of candidate parents present in the population was then calculated for each cohort as the total number of sampled candidate parents present in the population divided by 0.75. Notice that previous work has demonstrated that the simulation outcome is relatively insensitive to the number of candidates (Pemberton et al. 1999).

Because one of the input parameters for the simulation varied between years and sexes (i.e., the total number of candidate parents present in the population), to generate the critical δ values for 95% and 80% confidence levels, we carried out a separate simulation for each fawn cohort and for each sex of parent. Then, using these sex- and cohort-specific critical δ values, we performed a separate parentage analysis for each fawn cohort and each sex of parent. Initially, we ran a maternity analysis for each cohort to assign females to fawns with unknown mothers (i.e., those never observed in the field). From this, we retained only those mother–offspring associations that were assigned with 95% confidence by CERVUS. We then combined these assigned maternities with known maternities from field observations and, for each cohort, subsequently conducted the paternity analysis.

Statistical analyses

Although individual fitness (sensu Darwin) is not necessarily easily defined and its definition is highly context dependent, most authors agree that fitness equates to some measure of genetic contribution to future generations (Brommer et al. 2004), and empirical studies conventionally use LRS (usually defined as the number of offspring surviving to breeding age sired by a parent) as a valid single-generation proxy of long-term genetic contribution (see Clutton-Brock 1988; Brommer et al. 2004). In this study, because a proportion of the sampled fawns were caught as neonates for which the fate was unknown, we used male LBS, defined as the number of born

offspring sired by a male, as a proxy of individual male fitness. Although this measure does not integrate a juvenile survival component, fawn survival should be almost exclusively affected by maternal rather than by paternal influences in roe deer (Gaillard et al. 2000). Hence, the inclusion in the analysis of fawns caught during their first winter is unlikely to introduce any systematic bias in terms of the distribution of paternities among individual males.

After determining the distribution of paternities among males, we estimated YBS (the total number of paternities assigned at the 80% confidence level) for each known-aged male and for each reproductive season during which the male was considered as a candidate father. We also estimated LBS (the total number of independent offspring produced by a male during its life span) of each male for which data were available for the whole life span and which died of natural causes. We restricted LBS analyses to male cohorts born prior to 1999 for which all, or almost all, males had died at the end of the year 2005 (number of known candidate fathers for a given cohort still alive in 2005 is <4).

Variance in male LBS is the product of several components: the variance in LBS due to nonbreeders (individuals with LBS = 0) and, within breeders, the variation in reproductive life span (number of potential breeding seasons), annual fecundity (breeding success per season), and their covariance. To examine the contribution of these different components to the variance in male LBS, we used Brown's methodology for the analysis of the variance and covariance of products of random variables (Brown 1988; Brown and Alexander 1991; see also Coltman et al. 1999 for an application in Soay sheep). We also tested the hypothesis that male reproductive success was distributed randomly by comparing the observed number of assigned paternities with the number expected under a Poisson distribution with the same mean. Finally, we estimated the opportunity for sexual selection in roe deer by calculating the standardized variance in male reproductive success (I_m), that is, the ratio of variance in male reproductive success to the square of the mean male reproductive success, which represents an upper limit to the strength of directional sexual selection (Wade and Arnold 1980). However, this measure of opportunity for sexual selection does not take into account variation in female reproductive success, and so we also calculated the ratio of the total opportunity for sexual selection in the 2 sexes (I_m/I_f; Wade and Arnold 1980), which should be positively correlated with the intensity of sexual selection (Clutton-Brock 1983, 1988). For that, we estimated female LRS on 28 known-aged females, based on direct observation of fawns with their mothers in late September (Kjellander 2000; Kjellander et al. 2004; Vanpé C, unpublished data). We considered the number of fawns observed at the end of September to represent the number of weaned offspring for a given female observed at least 3 times with the same number of fawns at heel. Females were born from 1988 to 1998. We used only does for which data were available for the whole life span and which died of natural causes.

RESULTS

Test of microsatellite markers

Between 2 and 8 alleles per locus were identified (mean = 4.23) and expected heterozygosity ranged from 0.097 to 0.790 (mean = 0.527) among the 22 microsatellite loci (see supplementary material 2). There was no significant heterozygote excess or deficit at any single locus, nor over all loci combined ($P > 0.05$), except for the HUJ1177 locus (test of heterozygote deficit: $P = 0.022$). After correction for multiple comparisons (231 tests; critical $P = 0.000216$, minimum observed $P = 0.00043$), there was no evidence for significant linkage disequilibrium between any pair of loci, except for HUJ1177 × Roe5 ($P = 0.00022$). Finally, the estimated frequency of null alleles was negative or low (frequency < 0.02), except for HUJ1177 (frequency = 0.12). Hence, we decided to remove the HUJ1177 locus for parentage analysis. The total exclusionary power of the 21 retained microsatellites was 0.999675 when one parent was known and 0.985035 when both parents were unknown. The probability of identity over all loci was 5.14×10^{-12} among all individuals and 1.10×10^{-5} among siblings.

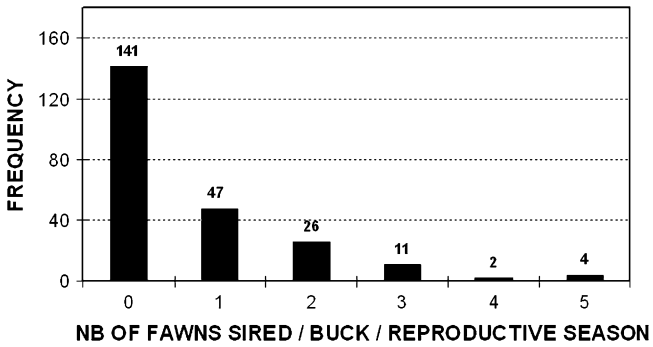

Figure 1
Frequency distribution of paternities assigned per buck (>1 year of age) and per year (assignments at the 80% confidence level) pooled over all years for all known-aged males ($N = 206$). Numbers above bars give exact frequencies.

Distribution of paternities between males and variance in male YBS

Of the 605 fawns sampled between 1988 and 2005 (see supplementary material 1), the mother's identity was known from behavioral observations for 267. From the maternity analyses performed using CERVUS, we identified the mother of a further 15 fawns at the 95% confidence level. We were then able to assign paternity to 442 fawns at the 80% confidence level (73% of the total 605), of which 235 were also assigned at the 95% confidence level (see supplementary material 1). Because very few fawns were sampled and assigned fathers from 1988 to 1991 ($N < 13$ at the 80% confidence level) compared with the potential number of fawns born in the population during these years of high density (see supplementary material 1), we removed these 4 years from the subsequent analyses of male YBS and LBS so as not to bias the results toward nonbreeding males. Sample size was thus 428 paternities assigned at the 80% confidence level (100 from known-aged males), of which 232 were also assigned at the 95% confidence level (60 from known-aged males).

Within a single reproductive season, the number of paternities assigned per known-aged male and per year ranged from 0 to 5 fawns ($N = 231$, mean ± standard error [SE] = 0.69 ± 0.07; see Figure 1). After removing all fawns with unknown mothers ($N = 37$), the fawns of a single known-aged male involved up to 3 different females but note that this is a conservative value.

Variance in male LBS

Of the 231 sampled candidate fathers, we could estimate the number of paternities assigned per male over the whole life span (LBS) for 24 candidate fathers (of which 9 were known-aged males). Of the 109 paternities assigned at the 80% confidence level to these 24 males, 66 were also assigned at 95% confidence level, 24 had an unknown mother, 77 had a known

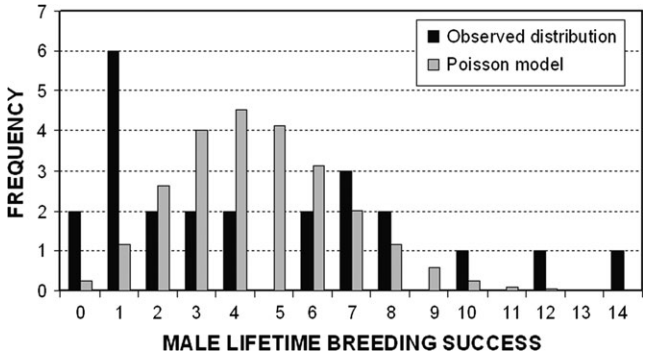

Figure 2
Comparison of the observed frequency distribution of LBS among bucks (both with known age and estimated age, $N = 24$) with a Poisson distribution with the same mean. We used only bucks for which data were available for the whole life span, which died of natural causes, and whose cohort was entirely, or almost entirely, extinct by the end of 2005. Black bars represent observed distribution; gray bars represent Poisson distribution with the same mean.

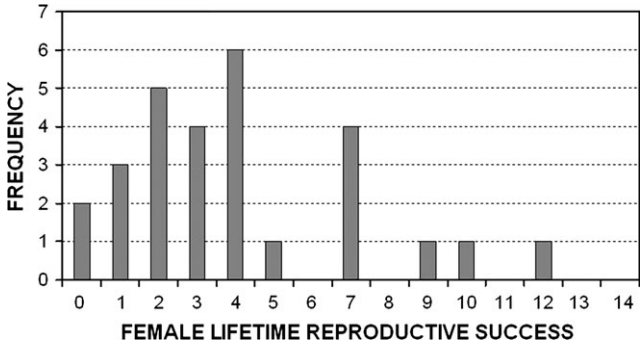

Figure 3
Distribution of LRS among known-aged does ($N = 28$). Data were based on direct observations of weaned fawns at heel at the end of September. Females were born between 1988 and 1998. We used only does for which data were available for the whole life span and which died of natural causes.

mother based on behavioral observations, and 8 had a known mother based on maternity analyses. LBS among all males ranged from 0 to 14 (mean ± SE = 4.54 ± 0.80, variance = 15.5; see Figure 2). The distribution of paternities over the lifetime deviated significantly from a Poisson distribution of the same mean ($\chi^2 = 8.05$, degrees of freedom = 1, $P = 0.0045$), indicating that LBS was not randomly distributed among bucks (see Figure 2). The 3 most successful males (i.e., about 13% of the 24 candidate fathers considered in LBS analyses) sired at least 10 fawns each, totaling 36 fawns together, which represents 33% of the assigned fawns. When we removed nonbreeders ($N = 2$), the mean LBS (±SE) was 4.95 ± 0.82. The 2 components of male LBS varied widely between individuals: reproductive life span ranged from 2 to 11 years (mean ± SE = 6.38 ± 0.59), whereas fecundity ranged from 0 to 1.6 fawns sired per year of reproductive life (mean ± SE = 0.67 ± 0.09). We calculated that about 88% of the variance in male LBS was due to breeders (that sired at least one fawn during their lifetime) and 12% to nonbreeders (that failed to breed at all). In addition, among breeders, variation in average fecundity contributed most to the variance in male LBS (56%), whereas variation in reproductive life span contributed somewhat less (33%), and the covariance between these 2 components contributed only 11%. The number of successful breeding years of a male was highly positively correlated to its reproductive life span (Spearman rank correlation test: $r_S = 0.67$, $P < 0.001$).

When considering only known-aged males ($N = 9$), the results followed an almost identical pattern, as LBS still ranged from 0 to 14 fawns (mean = 4.78, variance = 20.69), reproductive life span also ranged from 2 to 11 years (mean = 5.33, variance = 8.75), and annual fecundity ranged from 0 to 1.6 fawns (mean = 0.83, variance = 0.33). Furthermore, in this sample subset, about 80% of the variance in male LBS was due to breeders, of which variation in reproductive life span and variation in average fecundity contributed, respectively, to 34% and 54%. Consequently, we chose to consider LBS data for both known-aged and estimated age males in the following analyses of opportunity for sexual selection.

Opportunity for sexual selection

The opportunity for sexual selection was calculated both as the standardized variance in male LBS (I_m) and as the ratio of the standardized variance in male LBS to the standardized variance in female LBS (I_m/I_f). Based on LBS, I_m was 0.75 when considering all males and 0.60 when considering successful breeders only. This indicated that only a little of the standardized variance in LBS among all males was due to the inclusion of individuals that obtained no matings (I_m among successful breeders = 80% of I_m among all males). Early mortality also affected the opportunity for sexual selection. When only individuals with a reproductive life span superior or equal to 4 years were included ($N = 18$), I_m was 0.52, which is equal to 69% of the standardized variance in LBS among all males. LRS of known-aged female roe deer (see Figure 3) was found to range from 0 to 12 fawns ($N = 28$, mean = 4.19, variance = 9.27). Consequently, we estimated that the standardized variance in female LRS (I_f) was 0.53 and hence, the variance ratio I_m/I_f was 1.42.

DISCUSSION

In this paper, we used molecular paternity analysis to provide the first information on variance in male reproductive success and the opportunity for sexual selection in an ungulate species with low sexual size dimorphism. As expected, in line with the low level of sexual size dimorphism of roe deer (Andersen et al. 1998), we obtained a low standardized variance in male LBS, characteristic of a weakly polygynous mating system with a low opportunity for sexual selection.

Our results revealed that there was significant reproductive skew in roe deer, with several males siring no fawns or only one fawn and the most successful males siring up to 14 offspring over their lifetime (mean = 4.54, variance = 15.5). The maximum number of offspring sired per male was, however, lower in roe deer than in more sexually dimorphic ungulate species. In red deer, based on behavioral observations, Clutton-Brock et al. (1988) have reported that LRS varied from 0 to 32 calves surviving to the age of 2 years (mean = 5.41, variance = 41.9) among mature stags. In Soay sheep, male LRS ranged from 0 to 19 offspring (mean = 0.73, variance = 3.53; Pemberton et al. 1999 based on molecular tools).

One striking result from this study is that the variance in male LBS among breeders was a result of both variation in average fecundity (56%) and variation in reproductive life span (33%). This is in contrast to highly polygynous mammals, where variation in annual fecundity is usually the single largest component of fitness variation among breeding males (Clutton-Brock 1988), possibly because the age of successful reproduction is usually limited to a few years in these species. In red deer, for example, based on behavioral estimates of

male LRS, Clutton-Brock et al. (1988) reported a contribution of 32% for variance in annual fecundity, but of only 7% for variance in reproductive life span. Variance in longevity accounted for about 25% of the variance in male LRS in American pronghorn *Antilocapra americana* (Ord 1815), an ungulate with a level of sexual size dimorphism intermediate between red deer and roe deer (Byers 1997).

We also estimated the standardized variance in LBS (I_m), which represents an upper limit to the strength of directional sexual selection, to infer the opportunity for sexual selection in this territorial ungulate. A truly monogamous mating system should have an I_m value of zero, whereas mating systems with moderate to strong levels of polygyny should have positive I_m values (e.g., ranging from 5 to 50 in pinnipeds: Boness et al. 1993). As expected, in line with the low level of sexual size dimorphism of roe deer (Andersen et al. 1998), we obtained a low value of I_m (0.75 when considering all males and 0.60 when considering successful breeders only), characteristic of a weakly polygynous mating system. To take into account variation in female reproductive success, we also calculated the ratio of the total opportunity for sexual selection in the 2 sexes (I_m/I_f). We estimated that the standardized variance in female LRS (I_f) was 0.53 and the variance ratio I_m/I_f was 1.42. In polygynous species, I_f is expected to be lower than I_m (Clutton-Brock 1988). Our results supported this prediction, but interestingly, the difference between sexes was very low compared with highly dimorphic species (e.g., in red deer, $I_m/I_f =$ 9.85 and 3.53 based on behavioral observations of LBS and LRS, respectively; Clutton-Brock et al. 1988). Hence, again, these results support our prediction of a low level of polygyny and a low opportunity for sexual selection in roe deer.

Note, however, that because we succeeded in assigning paternity to only 73% of the sampled fawns and because not all fawns born in each cohort were sampled, we have certainly underestimated the YBS and the LBS of most males. In particular, we have likely overestimated the number of nonbreeding males. Indeed, we actually found that a surprisingly high proportion of the variance in male LBS (i.e., 12%) was due to nonbreeders that failed to sire any fawns during their lifetime. We have probably also underestimated the maximum number of fawns that a male can sire per year and during his lifetime. For example, one male, which was not included in YBS analyses because his age was estimated, sired up to 6 fawns per year and one male, which was not included in LBS analyses because he died during hunting aged 9 years, sired 15 fawns during his lifetime. However, although the mean LBS was clearly underestimated, it is unclear whether the variance was under- or overestimated. Also, the results are in agreement with predictions based on the current knowledge of roe deer life history (see Hewison et al. 2005) and on the low level of sexual size dimorphism in this species. Finally, the underestimation of mean male LBS should lead to an overestimation of the ratio I_m/I_f. Hence, our result is conservative, further supporting the prediction of a weakly polygynous mating system in roe deer.

In addition, although female LRS estimate was based on the number of weaned fawns at heel at the end of September, our measure of male LRS did not include an offspring survival component. As previously mentioned, this is not expected to affect variance in male LRS much (Gaillard et al. 2000) because male ungulates generally exert little influence on the survival of their offspring, so that differential genetic success arises primarily from differences in their mating contributions (Owen-Smith 1977). In contrast, offspring survival may be the most important component of variation in female reproductive success in large mammals (e.g., in red deer: Clutton-Brock et al. 1988; roe deer: Gaillard et al. 2000). In roe deer, the most critical stage for fawn survival is concentrated in the neonatal period during the first months of life (Gaillard, Andersen, et al. 1998; Linnell et al. 1998). Hence, by measuring female LBS as the number of fawns at heel at the end of September, we captured most of the variance in female LRS due to fawn survival.

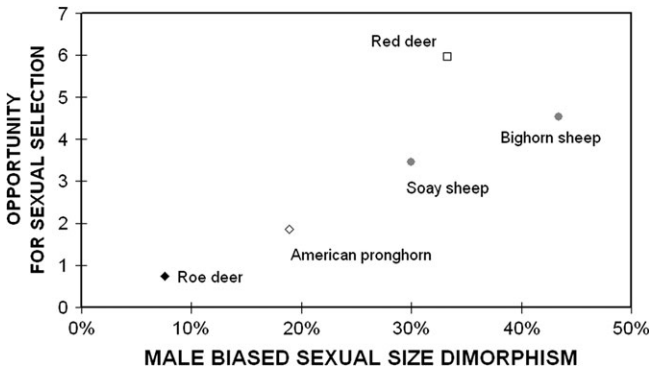

Figure 4
Opportunity for sexual selection in relation to the degree of male-biased sexual size dimorphism across different ungulate species. Note: Sexual size dimorphism data are estimated from mean male and female body mass data from Weckerly (1998). Estimations of the opportunity for sexual selection are based on published data of standardized variance in male LRS or LBS among all males (I_m): for roe deer (this study), for red deer (Marshall 1998), for Soay sheep (Coltman et al. 1999), for bighorn sheep (Coltman et al. 2002), and for American pronghorn (Byers 1997). Filled diamonds: territorial species; filled circles: tending/roving species; open squares: harem-holding species; and open diamonds: species with a mixed territorial/harem-holding mating system.

Jarman (1983) suggested that there is a continuum of sexual selection intensity in African antelopes, from monogamous and monomorphic species to highly polygynous and dimorphic species. We investigated whether this hypothesis was supported in ungulates in general by comparing published values of I_m, preferentially based on genetic paternity analysis, for species with varying levels of sexual size dimorphism (see Figure 4). In agreement with the predicted pattern, studies of ungulates with moderate to high male-biased sexual size dimorphism (males >30% heavier than females) reported much larger values of I_m than the value we obtained for roe deer (see Figure 4). Notice that these values are, however, lower ($3 < I_m < 6$ among all males) than those of pinniped species with moderate to strong levels of polygyny ($I_m >$ 5; Boness et al. 1993). Interestingly, the values obtained by Byers (1997) for the American pronghorn based on behavioral observations of mating success ($I_m = 1.08$ when considering the number of matings but 1.87 based on the number of offspring surviving to weaning; $I_m/I_f = 1.44$) were quite similar to the values we obtained for roe deer. Unfortunately, there is a lack of genetic data on standardized variance in male LBS of monomorphic and monogamous ungulate species in the literature for comparison with roe deer. However, we can expect that the value of I_m for such species may be even lower than the value we found in roe deer, converging toward zero. We therefore suggest that, along a continuum of opportunity for sexual selection in ungulates from monogamous and monomorphic species to highly polygynous and sexually dimorphic species, roe deer occupy an intermediate position, which is likely to be closer to monomorphic species than to highly dimorphic species. Our results also seem to support the view that territorial species such as roe deer or the American pronghorn (the American pronghorn has a mixed territorial/harem-holding mating system; see Byers 1997 for more details) tend to have a lower opportunity for

sexual selection than species with dominance rank–based mating systems (e.g., harem holding, roving) such as red deer, bighorn sheep, or Soay sheep. It is, however, less clear whether, for a given level of polygyny, sexual size dimorphism, variance in male reproductive success, and the opportunity for sexual selection should be consistently higher for species with dominance rank–based mating systems compared with territorial species (Clutton-Brock 1988). Much more data for ungulate species exhibiting various levels of sexual size dimorphism and different mating systems are needed to investigate this issue.

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SUPPLEMENTARY MATERIAL

Supplementary materials 1 and 2 can be found at http://www.beheco.oxfordjournals.org/

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