Mating Group Size and Stability in Reindeer *Rangifer tarandus*: The Effects of Male Characteristics, Sex Ratio and Male Age Structure

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Abstract

In polygynous mating systems, males compete intensely for mates and may mate several females during a single reproductive season. Accordingly, factors influencing the ability of males to control a larger number of females during the breeding season can provide information on the processes underlying sexual selection. In ungulates, age, body mass and social rank are considered good predictors of the reproductive success of males, but how male age structure and sex ratio in the population influence mating group (MG) dynamics has received little empirical testing. Between 1996 and 2005, we manipulated male age- and sex structure and monitored MG dynamics in a reindeer (*Rangifer tarandus*) population. We investigated the influence of male characteristics, percentage of males and male age structure on MG size and stability. We found that males with higher social rank (that were also older and heavier) controlled larger MGs (therefore had greater mating opportunities) and had more stable MGs (corresponding to a higher ability to maintain and control females) than males of lower social rank. Moreover, MG size and MG stability decreased as the percentage of males in the population increased, most likely resulting from greater male–male competition and increased female movements. Male age structure did not influence MG stability. Given the positive relationship between mating success and MG size (and likely MG stability), frequent female movements and intense competition among males to control females seem to be the principal components of reindeer MGs dynamic.

Introduction

The evolution of sexually selected traits is driven by contests over mating opportunities and/or by mate choice (Darwin 1871; Qvarnstrom & Forsgren 1998). In sexually dimorphic and polygynous species, the reproductive success of males varies more than that of females (Trivers 1972; Pemberton et al. 1992). Hence, males compete for access to females, whereas females generally carry out mate choice, selecting for male traits correlated with individual quality (Andersson 1994), such as characteristics conferring a high social rank or resistance to pathogens.

Male mating success varies according to ecological and phylogenetic factors that determine the distribution of females in oestrus and the amount of time and energy males can devote to defending mating access.
In many ungulates, mating groups often contain multiple males, although one male generally monopolizes most or all matings at any given time (Clutton-Brock 1989). The monopolization of females in oestrus appears to be mainly determined by the ability of males to keep other males away, which is strongly correlated with fighting abilities and often social rank (Roed et al. 2002; Pelletier & Festa-Bianchet 2006). Social rank is often correlated with conspicuous secondary traits such as body mass, body size and antler or horn size (Clutton-Brock et al. 1980; Barrette & Vandal 1986; Pelletier & Festa-Bianchet 2006). The degree of monopolization of females by males also depends on the operational sex ratio, the ratio of males to females that are ready to mate, which is strongly affected by the distribution of fertile females in time and space (Emlen & Oring 1977; Carранza 2000). The movements of males during the mating season are therefore strongly influenced by the need to search for, and herd together receptive females (Espmark 1964a; Clutton-Brock et al. 1982; Forsyth et al. 2005). Females often move among groups during the mating season, possibly to avoid harassment by young males (Clutton-Brock et al. 1996; Holand et al. 2006) or search for high-quality mates (Byers 1997), among other factors (see also Stöpher et al. 2011). Accordingly, the composition of the mating group (the number of females and the number and age structure of the males) as well as male characteristics may have a strong influence on male reproductive effort (Tennenhouse et al. 2011), and possibly on their reproductive success. Furthermore, social rank has been reported to be closely linked to reproductive success (Clutton-Brock et al. 1982; Roed et al. 2002; Pelletier et al. 2006).

The factors affecting social rank in male reindeer (*Rangifer tarandus*) are similar to other ungulates and include body mass, antler size and age (Bergerud 1974; Reimers 1983; Skogland 1989). Reindeer are polygynous ungulates (Jarman 1983; Skogland 1989) that form harems during the rut (Espmark 1964a). Age has been suggested to be one of the main factors determining success in male–male agonistic encounters in this species, allowing older males to control larger harems (Espmark 1964b; Skogland 1989). However, within a cohort, male social rank has also been reported to play a major role in determining mating success, as dominant individuals generally gain more matings than subordinates (Hirotani 1994).

Here, we tested the influence of male characteristics (age, body mass and social rank) and population structure (percentage of males and male age structure of the population) on mating group size and mating group stability. We used mating groups’ dynamics data from a semi-domesticated reindeer population that has been monitored during the rut between 1996 and 2005. Male age structure refers to one of the following three categories: only young, only adult and a mix of young and adult males. Mating group size was measured by the number of females in oestrus controlled by a male and mating group stability by the ability of a given male to control or keep females during their receptive period in his vicinity. Because movements among harems by females may reflect their effort to look for high-quality males (Byers 1997) and thereby partly determine mating group dynamics, we expected high-quality males to have a greater ability to control females. Accordingly, we tested the following three predictions: (1) Male quality (measured by their social rank, their age or their body mass) will be positively associated with mating group size and stability; (2) as the percentage of males in the population increases, the average mating group size will decrease and females will move more between groups (i.e. a decrease in mating group stability); (3) mating group size will decrease, and females will move more between mating groups when there are only young males in the population or when there are both young and adult males in the population as compared to years with adult males only. This may occur primarily because of increased harassment by young males that are less effective in holding large mating groups (Ozoga & Verme 1985). Moreover, because of the need for increased sampling efforts to find higher-quality males, females avoid mating with young males (Holand et al. 2006).
Methods

Study Area and Study Population

This study was conducted at the Kutuharju Field Reindeer Research Station in Kaamanen: northern Finland (69°N, 27°E). Reindeer used two large fenced enclosures during the rut, the north-west section (Lauluvaara ~ 13.8 km²) and the south-east section (Sinioaivi ~ 15 km²). The area is characterized by open birch Betula spp. and pine Pinus sylvestris forests with many bogs and lakes. We used a semi-domesticated reindeer population consisting of about 100 animals all of known age that has been studied since 1996. After the breeding season in late Oct., the animals are herded and put in a winter grazing area (15 km²) where they are supplementally fed concentrate, especially during harsh winter years. Females are transferred into a calving enclosure (approximately 0.5 km²) in late April where newborn calves are captured, sexed and marked with ear tags. The enclosure was surveyed daily, so that calving date is known for all individuals. The calving season occurs from May to early June.

Females are slaughtered at the age of 10–12 yr when they start showing signs of reproductive senescence. The age structure of females during the rut has been kept rather stable over the years. The age of females varied between 6 mo and 12½ yr. Females usually start to reproduce at 1½ yr old (Skogland 1989). They were all individually marked with uniquely coded collars. During 1996–2005, the composition of the male segment of the population was manipulated prior to the rut to obtain different age structures and percentage of males in the herd (Table 1). The male age structure was classified into three categories: adults (≥3.5 yr old), young males (<3.5 yr old) and a mixture of young and adult males (Table 1). Over the years, the proportion of males in the herd varied between 4 and 28%, and the proportion of adult males from 0% to 100% (Table 1). Males were all fitted with VHF radio collars (Televilt Co., Lindesburg, Sweden).

Data Collection

During the rut, from late Sep. to late Oct., each radio-collared male was located nearly daily using ground tracking. Every individual associated with the radio-marked male, and considered as part of the same mating group, was recorded. A reindeer mating group was defined as a group with at least one sexually mature male and one sexually mature female, with relatively consistent internal spacing and with individuals moving in roughly the same direction at a similar rate (or all stationary) (Creel & Winnie 2005). Thus, the composition of each mating group was established daily, enabling us to monitor the daily movements of females between mating groups and the number and identity of all subordinate males within the groups. Efforts were made to record most of the movements of individual females. For each male holding a mating group, we calculated the number of days that an individual female spent with him. We also estimated the frequencies of movements from one mating group to another by each female. If two or three males were present in the same mating group on a given day, the score (i.e. the number of days spent by each female in a mating group) was attributed to the highest ranked male.

Table 1: Annual sex composition and male age structure of semi-captive reindeer in the two experimental enclosures of the Kaamanen Experimental Reindeer Station, Finland, 1996–2005. Three male age structures are used: M = mixed age structure, Y = young males only and A = adult males only. Data for 1998 are not available.

<table>
<thead>
<tr>
<th>Year</th>
<th>Location</th>
<th>Females (N)</th>
<th>Males (N)</th>
<th>Number of males by age class (in years)</th>
<th>Percentage of males</th>
<th>Male age structure</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.5</td>
<td>2.5</td>
<td>3.5</td>
</tr>
<tr>
<td>1996</td>
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<td>43</td>
<td>6</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
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<td>Lauluvaara</td>
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<td>6</td>
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<td>0</td>
</tr>
<tr>
<td>1997</td>
<td>Sinioaivi</td>
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<td>18</td>
<td>9</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
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<td>47</td>
<td>4</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
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<td>Sinioaivi</td>
<td>75</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2000</td>
<td>Sinioaivi</td>
<td>75</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
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<td>11</td>
<td>11</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2002</td>
<td>Sinioaivi</td>
<td>92</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>2003</td>
<td>Sinioaivi</td>
<td>53</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>2004</td>
<td>Sinioaivi</td>
<td>49</td>
<td>4</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2005</td>
<td>Sinioaivi</td>
<td>55</td>
<td>17</td>
<td>10</td>
<td>4</td>
<td>1</td>
</tr>
</tbody>
</table>
Behavioural Observations and Social Rank

Matings and agonistic behaviours among males were recorded using all-occurrences sampling (Martin & Bateson 2007), whereby every instance of the behaviours was recorded. The most commonly observed agonistic interactions were displacement and chasing, and often sparring among young males. An agonistic interaction was considered resolved if one individual (the winner) clearly supplanted the other (the loser) who then moved away. A social hierarchy among males for each enclosure and each year separately was established based on the outcomes of agonistic interactions, using the methodology of De Vries (1995, 1998). This method uses win–lose matrices of interactions observed in a given year to rank individuals based on observed and expected dyadic relationships. Using Matman 1.0 for Windows (Noldus 1998), we first tested the linearity of the dominance hierarchies (De Vries 1995, 1998). If dominance hierarchies were significantly linear based on the improved Landau’s index of linearity (De Vries 1998), individuals were ordered in hierarchies. Matrix size varied among years, and thus, social ranks were transformed according to the formula:

$$\text{Standardized social rank} = 1 - \left( \frac{\text{rank} - 1}{N_i} \right)$$

where $N_i$ was the number of individuals in each matrix. Thus, social rank varied between 0 (subordinate) and 1 (dominant). This formula has been slightly modified from Côté (2000) to account for the small matrix size that affected the standardized social rank value of the most dominant male. In most years, few males were available (Table 1), and based on the agonistic and intersexual interactions, we easily identified a dominant male each time a group was observed.

Mean gestation length of females in this population was estimated, based on the average of 2 yr, at 222 d using birth dates of calves, paternity assignment tests and the date of observed copulations (Roed et al. 2002). By backdating from calving date and using the mean gestation length, we determined the oestrus period of each female estimated as the potential conception date ± 3 d, hereafter called ‘oestrus week’ (see also Holand et al. 2006; Tennenhouse et al. 2011).

Different Measures of Mating Group Dynamics

Using the daily composition of each mating group, we calculated the number of days that each female spent with a male during her oestrus week, from which we derived 2 (related) measures of mating group size and 2 (related) measures of mating group stability.

Mating Group Size Measure 1 (MG1)

The daily number of oestrus females in a mating group, corresponding to the number of oestrus females seen each day with each harem holder. A harem holder is the male identified as the dominant male in a mating group and is seen defending and controlling females.

Mating Group Size Measure 2 (MG2)

The annual number of oestrus females seen with each male. This is the sum of all oestrus female days for each male during the breeding season, corresponding to the number of mating opportunities for each male [\(\text{MG2} = \sum \text{(MG1)} \) for one male and one breeding season].

Mating Group Stability Measure 1 (MGS1)

The daily percentage of females leaving a mating group. For each day and for each harem holder, we divided the number of females leaving the group to another mating group by the total number of females in the group. This measure varied from 0 to 1, where 0 meant that no female left the group, corresponding to a perfectly stable mating group, and 1 meant that every female left the harem holder the next day, corresponding to a completely unstable mating group.

Mating Group Stability Measure 2 (MGS2)

The annual percentage of female movements is defined as the percentage of time each female left one mating group to another during the breeding season. For each male, we divided the number of departures (i.e. female leaving) of all females seen at least once with him by the sum of the total number of days each female spent in his mating group. This measure estimated the proportion of consecutive days spent by all females with each male during a breeding season. It varied from 0 when there was no female movement to 1 when for each day that a female spent with a male, she moved to another mating group the next day. Thus, smaller values of MGS2 correspond to more stable mating groups.

Statistical Analyses

We used generalized linear mixed models (GLMM; Proc GLIMMIX in SAS 9.2, SAS 2008) to test the effects of male characteristics (age, body mass or social rank), percentage of males and male age structure on
mating group size (MG1 and MG2; hereafter model 1 and model 2) and mating group stability (MG1 and MG2; hereafter model 3 and model 4, respectively). MG1 and MG2 were count data with a non-constant variance and errors not-normally distributed; we therefore used a GLMM with a log link function and a negative binomial error structure. A negative binomial distribution was preferred to the Poisson distribution to adjust for overdispersion (Littell et al. 2006). MG1 and MG2 were count data expressed as proportions with non-constant variance, thus we used a GLMM with a logit link function and a binomial error structure. Male identity was fitted as a random term in all models because of repeated measurements among individuals (Machlis et al. 1985). The number of females in each enclosure was also included as a covariate in models 1 and 2 to compare measures of group size on a common basis across years. Because of the high correlation among several of the predictor variables (body mass and age: $r = 0.90, p < 0.001$; body mass and social rank: $r = 0.46, p < 0.001$; age and social rank: $r = 0.55, p < 0.001$; percentage of males and number of females: $r = -0.43, p < 0.001$), we first checked for multicollinearity using the variance inflation factor (VIF) and the regression analysis of age, body mass, social rank, percentage of males and number of females on MG1 (VIF is independent of the response variable). To obtain a set of variables that are not collinear, we applied a backward selection process, whereby the term with the highest VIF value was eliminated first, the VIF values were recalculated for the remaining variables and the process repeated until all VIF were smaller than five (Montgomery & Peck 1992). We found VIF values to be high for age (VIF = 7.43) and body mass (VIF = 6.46) but small for social rank (VIF = 1.43), percentage of males (VIF = 1.47) and number of females (VIF = 1.25). When VIF values were recalculated after removing ‘age’ from the model, all the variables had a VIF value lower than 1.3, hence social rank, body mass, male percentage and number of females could be used simultaneously. Male age structure was constant for any year and included in all models, thus we did not fit year as a random term. The denominator degrees of freedom for the mixed models were calculated using the Satterthwaite approximation (Littell et al. 2006).

Overall, the sample sizes were 788, 755, 63 and 60 for MG1, MG51, MG2 and MG52, respectively, and the corresponding numbers of males’ identity were 39, 39, 43 and 40 because a number of males were used for more than 1 yr. Accordingly, we estimated the expected within-group correlation among measurements, the repeatability, as the proportion of the total variance accounted for by differences among groups (Nakagawa & Schielzeth 2010). Repeatability is estimated as the ratio of between-group variance by the total variance (meaning between-group variance plus within-group variance). All parameter estimates are reported with their 95% confidence intervals, and the predictive power ($R$) of the models is provided using the approach of Zheng & Agresti (2000) ($R$ is the correlation between the observed responses and the model predicted values). All analyses were performed in SAS version 9.2 (SAS 2008), and significance levels were set at 0.05.

### Results

The daily number of oestrus females controlled by a harem holder (MG1) increased with male social rank [estimate = 1.234; 95% CI (0.695; 1.772); Table 2a] and decreased with the percentage of males in the herd [$-0.049; 95% CI (-0.065; -0.033); Table 2a$]. The effect of the total number of females available annually was nearly significant ($p = 0.06; Table 2a$). The daily mating group size also varied with male age structure ($p = 0.03; Table 2a$), being smaller in years with only young males present as compared to years with both young and adult males (estimated difference $\pm SE = -0.40 \pm 0.18, t_{214.9} = 2.27, p = 0.02$). The repeatability was 0.25, while the predictive power was $R = 0.48$. Regarding the alternative measures of male quality, similar effects were obtained when substituting social rank by age ($0.308; 95% CI (0.173; 0.443)$) or body mass $[0.009; 95% CI (0.002; 0.015)]$.

**Table 2:** Generalized linear mixed model of the effect of social rank, body mass, percentage of males, male age structure and the total number of females in reindeer on (a) the daily number of oestrus females in a mating group (MG1) and (b) the annual number of oestrus females controlled by harem holder (MG2). ‘Male identity’ was entered as a random term in the model.

<table>
<thead>
<tr>
<th>Variables</th>
<th>df</th>
<th>$F$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) The daily number of oestrus females in a mating group</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male social rank</td>
<td>2</td>
<td>133.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Male body mass</td>
<td>1</td>
<td>114.7</td>
<td>0.47</td>
</tr>
<tr>
<td>Percentage of males</td>
<td>1</td>
<td>235.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Male age structure</td>
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<td>92.8</td>
<td>0.027</td>
</tr>
<tr>
<td>Number of females in the population</td>
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<td>36.2</td>
<td>0.063</td>
</tr>
<tr>
<td>(b) The annual number of oestrus females controlled by individual males</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Male social rank</td>
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<td>52.37</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Male body mass</td>
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<td>1.81</td>
</tr>
<tr>
<td>Percentage of males</td>
<td>1</td>
<td>39.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Male age structure</td>
<td>2</td>
<td>49.18</td>
<td>0.64</td>
</tr>
<tr>
<td>Number of females in the population</td>
<td>1</td>
<td>50.86</td>
<td>0.022</td>
</tr>
</tbody>
</table>
The annual number of oestrus females controlled by each harem holder (MG2) also increased with male social rank \([2.665; \text{95\%CI (1.837; 3.493); Table 2b, Fig. 1a}\] and decreased with the percentage of males in the herd \([-0.067; \text{95\%CI (0.895; -0.309); Table 2b, Fig. 1b}\]. The total number of oestrus female days controlled by harem holders annually was not influenced by male age structure \((p = 0.53; \text{Table 2b})\), but was positively influenced by the total number of females in the population \([0.017; \text{95\%CI (0.002; 0.031); Table 2b}\]. The repeatability was 0.38, while the predictive power was \(R = 0.77\). Again, similar results were obtained when substituting social rank by age \([0.585; \text{95\%CI (0.359; 0.811)}]\) or body mass \([0.022; \text{95\%CI (0.009; 0.036)}]\).

The daily percentage of females leaving a mating group (MGS1) was inversely related to male social rank \([-1.704; \text{95\%CI (2.256; -1.154); Table 3a}\], suggesting that mating groups controlled by high-ranked males were more stable, but was not influenced by the percentage of males in the herd, male age structure or the total number of females available in the population \((p > 0.05; \text{Table 3a})\). The repeatability was 0.05, while the predictive power was \(R = 0.26\). Substituting social rank by age or body mass also yielded a significant negative relationship with MGS1 \([\text{age: } -0.172; \text{95\%CI (0.327; -0.018); body mass: } -0.009; \text{95\%CI (0.017; -0.001)}]\). The annual percentage of female movements between mating groups (MGS2) was significantly influenced by male social rank \((\text{Table 3b})\) and percentage of males \((\text{Table 3b})\), but not by male age structure \((p = 0.20; \text{Table 3b})\) or number of females in the population \((p = 0.97; \text{Table 3b})\). The annual frequency of female movements was inversely related to male social rank \([-2.249; \text{95\%CI (-2.959; -1.539); Table 3b, Fig. 2a}\] and increased with the percentage of males \([0.033; \text{95\%CI (0.012; 0.054); Table 3b, Fig. 2b}\). The repeatability was 0.17, while the predictive power was \(R = 0.78\). Substituting social rank by age or body mass also yielded a significant negative relationship \([\text{age: } -0.379; \text{95\%CI (0.580; -0.178); body mass: } -0.012; \text{95\%CI (0.022; 0.003)}]\). Moreover, removing the percentage of males in the herd from the models yielded a significant effect of male age structure for both MGS1 \((F_{2,77.05} = 3.16, p = 0.05)\) and MGS2 \((F_{2,54} = 3.63, p = 0.03)\).

**Discussion**

We found that social rank (that was strongly associated with age and body mass) of the harem holder was consistently positively related to the number of oestrus females available in his mating group and the stability of the mating group as expected from prediction 1. Mating group size decreased and females moved more as the percentage of males in the population increased, supporting prediction 2, but not consistently so with variation in male age structure, which was contrary to prediction 3. Repeatability was generally high in our data (average of 0.21 for daily data and 0.27 for annual data), suggesting a tendency for some individuals to have greater effects on the observed patterns, for example, high-quality males could consistently control larger and more stable mating groups. Such high repeatability may lead to increased variance in mating success, and therefore increase the strength of sexual selection based on harem size more than expected.
Social rank, age and body mass were all positively correlated. Moreover, replacing social rank by age or body mass yielded a significant effect of age or body mass in the same direction. Accordingly, we will interpret the effect of male characteristics in a male ‘quality’ context, whereby ‘quality’ is used to rank individuals on a continuum scale (see Bergeron et al. 2011). That male quality consistently influenced mating group size and mating group stability was not surprising for a polygynous species like reindeer. To secure higher reproductive success, individual males should prevent other males’ access to females (Emlen & Oring 1977). On the other hand, females generally tend to move actively between groups and males also have to herd them. Hirotani (1989) suggested that female reindeer were choosing high-ranked breeding partners by moving between males. In lekking fallow deer (Dama dama), does changed territories about four times per hour (Clutton-Brock et al. 1992). However, Clutton-Brock (1989) suggested that differences in the reproductive success of males were more the result of male–male competition than female choice for a particular phenotype. Moreover, in red deer (Cervus elaphus), the activities of competing stags were reported to greatly influence harem membership (Clutton-Brock et al. 1982). In reindeer, estimates of mating group size of males are good predictors of their reproductive success, and the distribution of reproductive success is highly skewed towards the most dominant males (Hirotani 1994; Røed et al. 2002).

Controlling a mating group requires males to continuously chase rivals and herd females (Espmark 1964a; Clutton-Brock et al. 1982; Skogland 1989; Clutton-Brock & McAuliffe 2009). Harem holders must therefore fight with other males to maintain control of the harem (Espmark 1964a), and fighting can be energetically demanding (Clutton-Brock et al. 1979). The capacity to perform mating group tasks (chasing subordinate males, herding females, standing, grunting) depends mainly on energy reserves as these behaviours are performed almost continuously throughout the rut, a period when harem holders in most large herbivores almost stop feeding (Espmark 1964a; Miquelle 1990; Pelletier et al. 2009). Thus, the ability of harem holders to maintain a stable group depends on their vigour (Skogland 1989). As a result, energy requirements during the breeding season should be a function of the number of females

| Table 3: Generalized linear mixed model of the effect of social rank, body mass, percentage of males, male age structure and the total number of females in reindeer on (a) the daily percentage of females leaving a mating group (MGS1) and (b) the annual percentage of female movements between harems (MGS2). ‘Male identity’ was entered as a random term in the models |
|---|---|---|---|
| Variables | df | F | p |
| (a) The daily percentage of females leaving | | | |
| Male social rank | 1, 85.57 | 37.59 | <0.001 |
| Male body mass | 1, 70.19 | 1.51 | 0.223 |
| Percentage of males | 1, 237.1 | 2.22 | 0.137 |
| Male age structure | 2, 68.82 | 2.08 | 0.133 |
| Number of females in the population | 1, 43.7 | 1.56 | 0.219 |
| (b) The annual percentage of females leaving | | | |
| Male social rank | 1, 53 | 40.38 | <0.001 |
| Male body mass | 1, 53 | 0.08 | 0.782 |
| Percentage of males | 1, 53 | 9.64 | 0.003 |
| Male age structure | 2, 53 | 0.90 | 0.413 |
| Number of females in the population | 1, 35.21 | 0.00 | 0.967 |
controlled (Tennenhouse et al. 2011), the duration of control and the intensity of male–male competition. Reindeer are capital breeders, meaning that they use reserves stored during the preceding spring and summer for reproduction (Jönsson 1997). Our results therefore suggest that high ‘quality’ reindeer males have higher energy reserves or are better at converting stored energy into harem-holding activities such as the control of females’ movements. By having a greater ability to retain oestrus females in their group, more vigorous males increase their mating opportunities, which is likely to be correlated with their reproductive success (Roed et al. 2002).

In several large herbivore populations, it has been reported that mating group size decreases and females move more as the percentage of males in the population increase. In red deer, Bonenfant et al. (2004) found harem size to decrease with increasing proportion of adult males, and Bender (1996) found the number of bulls present in an elk population to be the key determinant of harem size, which also decreased with increasing bull/cow ratios. In reindeer, Roed et al. (2002) found that the largest mating group in a herd had the least skewed sex ratio towards males. Similar results were reported in feral horses Equus caballus where a negative relationship was found between mean harem size and adult male/female ratio (Kaseda & Khalil 1996). Decreases in harem sizes in the presence of increasing numbers of males (i.e. competitors) are likely due to the increased energetic demands of holding large mating groups (Clutton-Brock et al. 1982; Roed et al. 2002), which may offset the long-term reproductive advantages of large harem size. This ultimately supports the associated reduced mating group stability observed as a consequence of greater movements of females (Clutton-Brock et al. 1982). Indeed, increased male–male competition due to increasing percentage of males increases the energetic costs of excluding rivals to hold a larger mating group. This also reduces the level of attention to females who may then move more ‘freely’ to other groups. Harem size (total number of males and females in a mating group) was highly correlated with the number of oestrus females, MG1 ($r = 0.6$, $p < 0.001$). Moreover, when using harem size instead of MG1 as a response variable, results were similar and highly comparable [social rank: 1.042; 95%CI (0.749; 1.336); percentage of males: $−0.028; 95%CI (−0.037; −0.019)$; harem size being smaller in years with only young males present as compared to years with both young and adult males (estimated difference $\pm SE = −0.224 \pm 0.097$, $t_{222.6} = 2.31$, $p = 0.02$)]. This suggests that our index of mating group could also be representing harem dynamics, so that harem size can be predicted to increase with male quality and decrease with the percentage of males in the population.

Because of their immature behaviours, young males can generate stress and somatic costs to females (Valdez et al. 1991; Réale et al. 1996; Holand et al. 2006). In this context, one would expect mating group size to be smaller and females to move more when a greater proportion of young males is present. This, however, was not always the case as the movement of females did not generally vary with male age structure. This was likely due to age structure being confounded by male percentages, as removing male percentages from the models yielded significant effects of male age structure on MGS1 and MGS2. Moreover, our results could also be explained by the structure of the data, as we had only 1 yr with only adult males present. In fact, when the analyses were repeated excluding that year, we found as predicted that groups were less stable during years with only young males present as compared to years with mixed age groups (estimated difference for MGS1: $−0.25 \pm 0.13$, $t_{124.4} = −2.02$, $p = 0.05$; and for MGS2: $−0.37 \pm 0.16$, $t_{57} = −2.31$, $p = 0.03$).

Our study showed that male social rank and the percentage of males in the population consistently influenced mating group dynamics. Males with higher social rank (that were also older and heavier) controlled larger mating groups (or had greater mating opportunities) and had more stable mating groups (or had higher ability to maintain and control females) than males of lower social rank. Moreover, mating group stability decreased as the percentage of males in the population increased. Given the positive relationship between mating group size and mating success (Pemberton et al. 1992; Byers 1997), frequent female movements between mating groups and intense competition among males to control females appear to be the principal components of the mating group dynamics in reindeer. Clearly, because a larger harem may mean larger mating opportunities, harem size may provide an easy way to estimate the strength of sexual selection. Accordingly, a few males are highly successful at mating while many others are not (Wade & Shuster 2004). Despite the efforts of males to keep and control females, females could still move between harems, but whether such female movement could relate to female mate choice remains to be investigated. The mating tactics of reindeer may not have been properly classified, but while they are thought to engage in female defence polygyny, whereby males control access to females directly (sensu Emlen &
Oring 1977), our observations indicate greater fluidity in the structure of mating groups. This may suggest greater plasticity in mating tactics than previously thought (see Carranza 2000).

Acknowledgements

We thank Veijo and Mika Tervonen of the Finnish Reindeer Herder’s Association and their crew at the Kutuharju Experimental Reindeer Research Station for valuable assistance. Heikki Törma¨ nen in Kaama-­‐nu¨nen helped with logistic and assistance in the field. Many people helped with the fieldwork at Kutuharju over the years and we thank all of them. The Research Council of Norway, the Finnish Game and Fisheries Research Institute, the Norwegian Reindeer Husbandry Research Council and the Natural Sciences and Engineering Research Council (NSERC) of Canada supported this research. We are grateful to Sandra Hamel, Marco Festa-Bianchet, Christophe Bonenfant and an anonymous referee for valuable comments on a previous draft.

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