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Male age structure influences females' mass change during rut in a polygynous ungulate: the reindeer (*Rangifer tarandus*)

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Abstract The manipulation of the sex ratio and age structure in many managed ungulate populations calls for a better understanding of their potential consequences on females' condition and behavior during rut. During 1996–2002, we manipulated the male age structure and male percentage (nine treatments during 7 years) within an experimental herd of semidomestic reindeer (*Rangifer tarandus*) and investigated their influence on both the body mass change and the behavior of females during rut. On average, the females lost body mass ($-0.95 \pm \text{SE } 0.18$ kg) during rut, which we contend to reflect somatic costs. The females' losses increased as the percentage of

male decreased, but this was certainly ascribed to one treatment with high male percentage (27.7%) as compared to the others (ranging from 3.9 to 12.2%). Female losses were highest for treatments including both young and adult males as compared to only adult or only young males, and higher for treatments including only young compared to only adult males. This is supported by (1) the higher female harassment frequency when females are exposed to only young or a mixture of young and adult males as compared to only adults, (2) the higher female harassment frequency by young males as compared to adults in the mixed treatments, and (3) the reduced females' feeding activity in treatments including both young and adult males. We conclude that the male age structure during rut will influence the females' behavior and mass change and may have implications for females' life history and for population dynamics.

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Introduction

A female-biased sex ratio among adults and a skewed age distribution of males toward young have been reported in many managed ungulate populations (e.g., Caughley 1977; Cederlund and Markgren 1987; Lenvik and Aune 1988; Skogland 1989; Langvatn and Loison 1999). Such features are likely to increase the productivity, but evidence of negative influence on birth synchrony and timing (Noyes et al. 1996, 2002; Holand et al. 2003; Sæther et al. 2003) as well as on fecundity (Solberg et al. 2002) have recently been reported. In some extreme cases, the ungulate population can even collapse. For example, the highly skewed adult sex ratio in favor of females probably due to selective poaching of adult males led to a drastic decline in fecundity rate and thereby to a population decrease of the saiga antelope (*Saiga tatarica tatarica*) (Milner-Gulland et al. 2003). Female choice could be involved in such situations because female ungulates often try to avoid breeding with

young males (Clutton-Brock et al. 1992; Schwartz 1998; Komers et al. 1999). Hence, mate choice is condition-dependent because costs and benefits are likely to vary in relation to environmental and social conditions (Kvarnemo and Ahnesjö 1996; Jennions and Petrie 1997; Widemo and Sæther 1999). Individual quality may also influence female mate choice (Jennions and Petrie 1997; Widemo and Sæther 1999). Indeed, we expect females in good condition because of their resource surplus to be more willing to pay higher somatic costs when searching for mates than females in poor condition.

The harassment level of females imposed by the males may vary according to the level of intrasexual competition among males and to the females' own body condition (reviewed by Reynolds 1996). Empirical evidence suggests that young ungulate males have a less well-developed social rutting behavior causing extra stress (Clutton-Brock et al. 1992; Komers et al. 1999; Valdez et al. 1991; but see Shackelton 1991) indirectly affecting females' foraging activity and hence their postrut condition. Protection against harassment from young males leading to reduced somatic cost has been suggested as an important aspect in explaining the evolution of ungulate aggregation during rut (Clutton-Brock et al. 1992, but see Carbone and Taborsky 1995). Recent studies have estimated the reproductive effort of male ungulates during rut (Yoccoz et al. 2002; Myrsterud et al. 2003). To our knowledge, few empirical studies in ungulates have so far tried to quantify the potential somatic cost of females during the rut and tested whether the male environment affects this cost (but see Komers et al. 1999) and the females' behavioral response. As autumn body mass of northern and temperate female ungulates is a good predictor of reproductive performance the following summer (e.g., Mitchell et al. 1976; Lenvik and Aune 1988; Cameron et al. 1993; Festa-Bianchet 1998), the composition of the male segment during rut may have implications for females' life history and population dynamics. We report here the potential somatic rutting cost in reindeer (*Rangifer tarandus*) by addressing the following questions: (1) is there any body mass change for females during rut?; (2) does the body mass change vary with male percentage and male age structure?, and (3) does the male age structure affect the females' activity during rut?

Materials and methods

The study was conducted at Kaamanen Experimental Reindeer Station, Finland (69°N, 27°E) (Røed et al. 2002; Holand et al. 2003). During the rutting periods from 1996 through 2002, the composition of the male segment of the reindeer herd was manipulated (Table 1). Three male age structures were used: (1) only adult (≥ 3 years old) males present at rut, (2) only young males (1.5 years old) present, and (3) a mixture of male age classes, including both adult and young males, present (Table 1). The percentage of males (the number of males divided by the total number of reproductive animals) varied from 3.9 to 27.7% (Table 1).

The herd was confined to two fenced areas, Siniöivi (15 km²) and Luluvaara (13.8 km²), during the rutting periods (Table 1). One treatment was set up for each of the years in Siniöivi, whereas Luluvaara was only used in 1996 and 1997 (Table 1). The females in the experimental herd are normally slaughtered at an age of 10–12 years when they start to show signs of senescence. Hence, the age structure of females was rather stable (Table 1), whereas the body mass at rut varied between years (Table 1). Females were individually marked and weighed (to the nearest kilogram) before (15–20 September) and after (30 October–10 November) the rutting season. Because of some missing weights, not all females could be included in the analyses. Simultaneously, calves were also weighed, and we calculated their mean body mass change to assess yearly variation in grazing conditions during rut.

Behavioral data

Before rut, all males were fitted with radio collars, enabling us to track on a daily basis all mating groups, defined as a group of females with a dominant male present (Krebs and Davies 1993). After recording the composition of the mating group, females' activity and behavior were observed based on the focal animal technique (Martin and Bateson 1993). A randomly chosen female was observed for 15 min. Every 15 s, we recorded the activity of the female as rest, walk, stand, and eat, or as direct rutting behavior (i.e., rubbing antlers and investigating males). We also recorded antagonistic interactions with other females and males, and if the focal female was harassed (i.e., displaced or chased) by a male, and we noted the identity of the male. Scattered mating groups within the enclosure and short autumn days in northern Finland limited the number of observations. When possible, a new female was randomly chosen from the rest of the mating group after a 15-min break. All observations were conducted between 0900 and 1900 hours. Behavioral data were not collected during the 1998 rut due to lack of funding.

In the analysis, all focal observations containing "rest" were omitted, i.e., only the females' activity when on foot during the whole focal observation was used in the analyses. The rut was divided into three phases: prerut, peak rut, and postrut. Peak rut was calculated separately for each year based on the average date of the copulations observed ± 3 days. The prerut and postrut were defined as 1 week prior to and 1 week after peak rut, respectively. The focal observations not coinciding with these phases were omitted.

Statistical analyses

We assessed body mass changes during rut (i.e., body mass after rut minus body mass before rut), using a two-tailed one-sample *t* test for each treatment. Hence, a negative mass change in a given year for a given individual would

Table 1 Herd composition and females' characteristics during rut for the nine treatments used in the analyses

Treatment	Year	Location	Females (<i>n</i>)	Males (<i>n</i>)	Calves (<i>n</i>)	Number of males by age class					Females' characteristics		Male percentage	Male age structure
						1	2	3	4	5	Weight (kg±SE)	Age (years±SE)		
1	1996	Sinioivi	43	6	19	3	0	0	3	0	79.5±1.79	5.1±0.47	12.2	M
2	1996	Lauluvaara	46	6	24	6	0	0	0	0	76.9±1.45	5.1±0.43	11.5	Y
3	1997	Sinioivi	47	18	27	9	6	0	0	3	73.6±1.33	4.6±0.42	27.7	M
4	1997	Lauluvaara	47	4	27	4	0	0	0	0	75.8±0.44	4.5±0.44	7.8	Y
5	1998	Sinioivi	81	6	60	0	0	6	0	0	79.2±0.78	4.7±0.31	6.9	A
6	1999	Sinioivi	75	3	42	0	0	0	3	0	74.6±1.07	4.6±0.31	3.9	A
7	2000	Sinioivi	74	3	10	3	0	0	0	0	76.9±1.14	4.5±0.29	3.9	Y
8	2001	Sinioivi	79	11	57	11	0	0	0	0	83.6±0.81	5.2±0.30	12.2	Y
9	2002	Sinioivi	94	4	63	2	1	0	1	0	84.3±0.88	5.2±0.32	4.1	M

M Mixed age structure, *Y* only young males, *A* only adult males present

reflect a somatic cost. We used generalized linear mixed models to investigate whether the treatment effect could be attributed to the change in percentage of adult males, to the change in percentage of young males, or to the combination of both (assessed by including the interaction term between both variables in model 1). We further tested whether male age structure influenced the females' somatic cost (model 2). Females' reproductive status during rut (i.e., whether a female had a calf at heel or not) was included as covariate in the models. We used the age-specific female body mass (the body mass of the female adjusted for her age) in mid-September as an index of the female condition before rut (see, e.g., Weladji et al. 2002). We also included body mass change of female calves during rut as a proxy of the grazing condition (including range quality and potential direct weather effects) during rut because the heaviest male calves showed a tendency of rutting behavior in contrast to female calves (Ø. Holand, unpublished data). Because of repeated measurement on individual females across years, female identity was fitted in the models as a random term. We divided the experiment into two periods based on the female number as it nearly doubled from the first period (1996 and 1997) to the second period (1998–2002)

(Table 1), probably influencing the social setting. All variables, except male age structure [totally three levels; only young, only adults and mixed (including both young and adults)], period (two levels, 1 and 2) and reproductive status (two levels for calf at heel, present and none), were entered as continuous.

Because of a highly skewed distribution of the female harassment frequency data (582 focal observations with no harassment, 52 observations with one harassment, 31 observations with two harassments, 6 observations with three harassments, 7 observations with four harassments, and 8 observations with >4 harassments by males), we pooled the observations into two classes: (1) harassed by males and (2) not harassed by males. We used a generalized linear mixed model with a logit link function by applying the general linear model for mixture distributions (GLIMMIX) macro in SAS (1999) to assess the effect of male age structure on the female harassment by the males (a binomial response variable, harassed by males vs not harassed by males) and a generalized linear mixed model by applying the mixed procedure (SAS 1999) to assess the effect of male age structure on female time spent foraging, defined as number of foraging activity registered out of a

Table 2 Absolute change in body mass during rut (mean difference±SE) for females and female calves during the nine treatments

Treatment	Females			Female calves		
	Change in body mass (kg)	<i>t</i> value	<i>P</i> value	Change in body mass (kg)	<i>t</i> value	<i>P</i> value
1 (M)	-0.54±0.50 (<i>n</i> =41)	-1.08	0.290	7.38±0.73 (<i>n</i> =8)	9.21	<0.001
2 (Y)	-1.55±0.53 (<i>n</i> =36)	-2.94	0.006	4.78±0.69 (<i>n</i> =9)	13.11	<0.001
3 (M)	5.62±0.40 (<i>n</i> =47)	13.9	<0.001	8.83±0.60 (<i>n</i> =12)	16.54	<0.001
4 (Y)	2.25±0.47 (<i>n</i> =44)	5.93	<0.001	6.62±0.62 (<i>n</i> =11)	10.36	<0.001
5 (A)	-2.65±0.38 (<i>n</i> =71)	-6.96	<0.001	2.32±0.35 (<i>n</i> =33)	7.88	<0.001
6 (A)	0.51±0.30 (<i>n</i> =71)	1.67	0.099	4.60±0.65 (<i>n</i> =10)	5.71	<0.001
7 (Y)	-0.03±0.41 (<i>n</i> =69)	-0.07	0.944	5.00±1.46 (<i>n</i> =6)	5.70	0.002
8 (Y)	-3.10±0.26 (<i>n</i> =79)	-12.01	<0.001	3.83±0.49 (<i>n</i> =18)	7.21	<0.001
9 (M)	-4.50±0.44 (<i>n</i> =91)	-10.26	<0.001	3.17±0.38 (<i>n</i> =29)	7.33	<0.001

One-sample two-tailed *t* test results are presented, and the sample sizes are given in parentheses

M mixed age structure, *Y* only young males, *A* only adult males present

total of 60 registrations within a 15-min focal observation. In both models, we included rutting phase (three levels: prerut, peak rut, and postrut) and period (two levels: first period, 1996 and 1997, and second period, 1999–2002) as covariates in the model. Because of repeated measurement on individual females within a year and across years, female identity was fitted in the models as a random term. All explanatory variables, male age structure [totally three levels; only young, only adults and mixed (including both young and adults)], period, and rutting phase were entered as class. For the three mixed treatments (Sinioivi 1996, 1997, and 2002), we compared the harassment frequency of young (1.5 years old) vs adult (≥ 3.5 years old) males using a chi-square test. All statistical analyses were performed in SAS for Windows, version 8 (SAS 1999).

Results

Evidence of female mass change during rut

The females lost mass in 1996 (Lauluvaara), 1998, 2001, and 2002, and gained mass in 1997 only (Table 2), so that on average, females incurred a somatic cost during rut in all years (mean loss \pm SE=0.95 \pm 0.18 kg, $t_{548}=5.29$, $P<0.001$). The female calves gained mass during rut in all years (Table 2), 4.35 \pm SE 0.25 kg ($t_{136}=17.42$, $P<0.001$) on average.

Influence of male percentage and age structure on female change in body mass during rut

Increased percentage of males in the herd during the rut reduced the somatic cost (young: $F_{1,374}=5.30$, $P=0.0219$; adult: $F_{1,374}=16.77$, $P<0.001$) (Table 3, model 1). There was no significant interaction between the percentage of young and the percentage of adult males ($F_{1,374}=3.42$, $P=0.065$) (Table 3, model 1). Change in body mass during rut was influenced by the male age structure ($F_{2,375}=39.23$, $P<0.001$). The absolute somatic cost was significantly higher when only young males or both young and adult males were involved in the rutting season simultaneously as compared to when only adult males were present (Table 3, model 2; Fig. 1). It also appears that somatic cost was higher when both young and adult males were involved in the rutting season simultaneously as compared to when only young males were present (mean difference \pm SE=0.98 \pm 0.31, $t_{375}=3.17$, $P=0.002$, Fig. 1). These findings suggest that the presence of young males in the breeding stock was more costly for females during rut. The initial body condition (i.e., age-specific body mass) of the females significantly increased the mass loss (Table 3), and the females having calves at heel lost, on average, more mass during rut than females without calves (Table 3).

Table 3 Parameter estimates (least square estimates) with standard errors (SE) and P values for the mixed linear models (1 and 2) fitting the body mass change for female reindeer during rut

Term	Estimates	SE	P value
Model 1			
Intercept	-10.14	0.90	<0.001
Female age-specific body mass	-0.14	0.02	<0.001
Percentage of young males	0.12	0.05	0.022
Percentage of adult males	0.38	0.09	<0.001
Percentage of young males \times percentage of adult males	-0.03	0.01	0.065
Range condition index	1.62	0.18	<0.001
Calf at heel (none-present)	1.34	0.30	<0.001
Period (P1-P2)	-1.69	0.57	0.003
Model 2			
Intercept	-7.21	0.48	<0.001
Female age specific body mass	-0.15	0.02	<0.001
Male age structure (young adult)	-2.34	0.35	<0.001
Male age structure (mixed-adult)	-3.32	0.38	<0.001
Range condition index	1.66	0.12	<0.001
Calf at heel (none-present)	1.17	0.35	<0.001
Period (P1-P2)	0.45	0.50	0.371

Male age structure with three levels [young only, mixed (young and adult), and adult only], calf at heel with two levels (present, none), and period with two levels (P1 for period 1 and P2 for period 2) were entered as categorical variables. In the male age structure (model 2), the effects of "young" and "mixed" are contrasted with "adult." " \times " denotes the interaction between terms

Influence of male age structure on female activity during rut

The females were less frequently harassed by males when exposed to adults alone than when exposed to both young

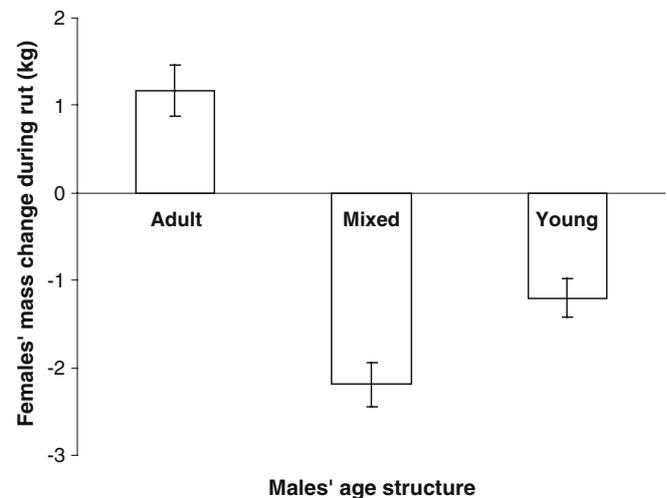


Fig. 1 Mean females' change in body mass as a measure of somatic cost (negative values denote body mass loss) (\pm SE) during rut in relation to the males' age structure during rut. The somatic cost is adjusted for female age-specific body mass, reproductive status, and yearly variation in range condition

and adults, i.e., the mixed age structure (estimated difference \pm SE=2.77 \pm 0.77, t_{436} =3.62, P <0.001) or to young males alone (estimated difference \pm SE=2.61 \pm 0.75, t_{436} =3.45, P <0.001), respectively (Fig. 2a). There was no difference in female harassment frequency by males when exposed to the mixed age structure as compared to young males only (estimated difference \pm SE=0.16 \pm 0.24, t_{436} =0.67, P =0.503) (Fig. 2a). The harassment frequency by males was lower in 1996–1997 as compared to 1999–2002 (estimated difference \pm SE=1.53 \pm 0.30, t_{436} =6.29, P <0.001), and the frequency was higher during prerut and peak rut as compared to postrut (estimated differences \pm SE=0.68 \pm 0.35, t_{436} =1.95, P =0.051 and 0.85 \pm 0.30, t_{436} =2.84, P =0.005, respectively). Within the mixed age structure, young males harassed the females more frequently than adult males (χ^2 =3.78, P =0.052).

The mean female foraging time, defined as the number of foraging activities registered out of a total of 60 registrations within a 15-min focal observation, was 49.35 \pm 0.74 (\pm SE) in the adult male treatments, 45.26 \pm 0.63 (\pm SE) in the

mixed age treatments, and 47.58 \pm 0.55 (\pm SE) in the young male treatments. The females spent less time foraging when exposed to the mixed age structure as compared to only young males (estimated difference \pm SE=2.27 \pm 0.83, t_{436} =2.75, P =0.006). Female foraging time was not significantly different for mixed vs adult male structures (estimated difference \pm SE=2.57 \pm 1.38, t_{436} =1.86, P =0.064). No difference in female time spent foraging when exposed to only adults vs when exposed to only young males was found (estimated difference \pm SE=0.30 \pm 1.33, t_{436} =0.22, P =0.823). The females spent less time foraging in prerut and peak rut as compared to postrut (estimate \pm SE=2.70 \pm 1.06, t_{436} =2.54, P =0.011 and estimate \pm SE=3.44 \pm 0.85, t_{436} =3.89, P <0.001), respectively, whereas no difference between 1996–1997 and 1999–2002 (estimated difference \pm SE=1.07 \pm 0.85, t_{436} =1.26, P =0.210) was found.

Discussion

Females' somatic cost during rut

Females' body mass change during rut showed great variations between years (Table 2). In a simple regression, 73% of the yearly females' mean body mass change was accounted for by the yearly mean body mass change in female calves during rut, suggesting a strong effect of yearly variation in range condition during rut. This was confirmed by the positive contribution of the mean yearly female calf body mass gain during rut on the body mass change in females (Table 3). The autumn of 1997 was exceptionally rich in mushrooms (Veijo Tervonen, personal communication), and consequently, the females were able to gain [on average, 4.03 \pm 0.34 kg (\pm SE)] mass during rut, as also confirmed by the extraordinarily high average body mass gain [7.87 \pm 0.45 kg (\pm SE)] in female calves that year (Table 2). Female calves actually gained body mass in all treatments (Table 2), indicating that the herd's autumn range normally has the potential to sustain body mass gain in reindeer. That females on average lost mass when female calves were gaining mass strengthens the idea that these are indeed somatic rutting costs.

During the rut, adult reindeer males in the same experimental herd lost around 20 kg, independently of the male percentage, which equals approximately 15% of their body mass, whereas the losses in 1.5- and 2.5-year-old males were negligible (Mysterud et al. 2003). Similar proportional reproductive effort has been reported earlier in reindeer (Espmark 1964; Kojola 1985) and in other polygynous adult male cervids [i.e., moose *Alces alces* (Solberg and Sæther 1994); fallow deer, *Dama dama* (Moore 1993); and red deer, *Cervus elaphus* (Yoccoz et al. 2002)]. The average absolute loss in adult females, excluding 1997, was 1.95 kg, representing around 2.5% of their body mass. Hence, the females' somatic cost during rut accounted only for about one sixth of the adult males' effort in relative terms, and underlines the sex differences in the timing of reproductive allocation.

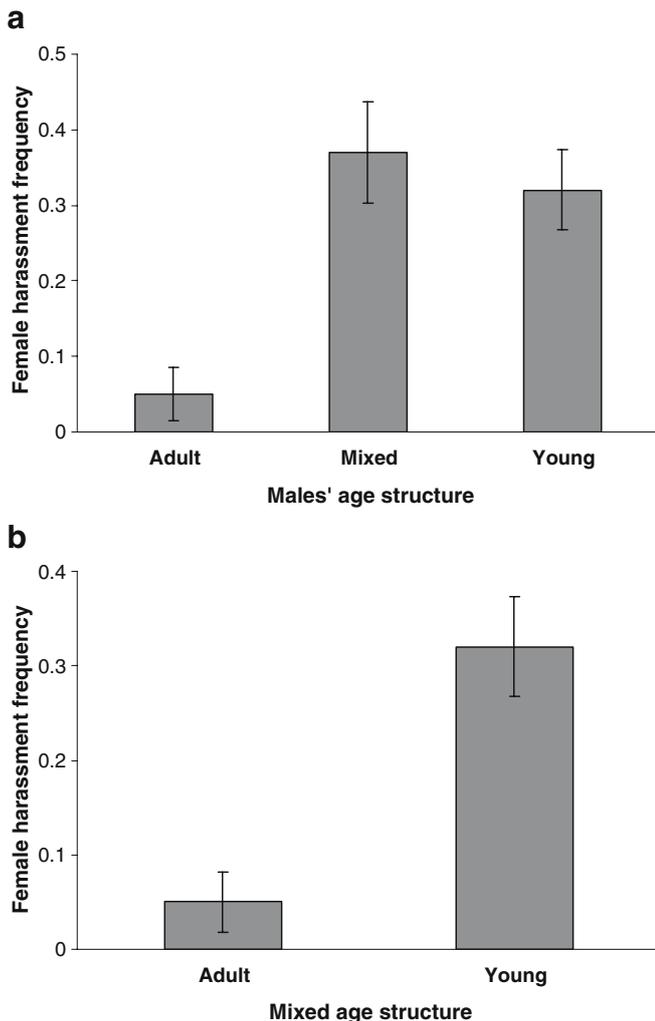


Fig. 2 Mean female harassment frequency per focal observation (\pm SE) (n =686) in relation to the males' age structure during rut (a) for the three age structures, i.e., young, mixed, and adults, and (b) for young and adult males in the mixed age structures only (n =284)

The importance of male age structure

Females seemed to pay a higher somatic cost during rut when exposed to a low male percentage, both young and adults (Table 3, model 1). The extremely low total male percentage (around 4%) in some of the treatments is probably close to a threshold where males, especially the young, are not able to serve all the females efficiently, creating extra stress among them. However, in only one treatment, the sex ratio (27.7% males) could be considered close to “natural” for wild reindeer populations without human impacts, in which adult male percentage is often around 40% (Skogland 1989). Indeed, in the eight other treatments, the male percentage ranged from 3.9 to 12.2%. We are thus unable to make a firm conclusion about the influence of male sex ratio on the females’ somatic costs from this experiment.

Treatments including young and adult males yielded the largest losses for females compared to only young males and to only adult males (Table 3, model 2; Fig. 1). In addition, treatments including only young males yielded larger losses compared to only adults (Table 3, model 2; Fig. 1). This accords with the suggestion of Komers et al. (1999) that female fallow deer in a lek mating system avoid young males to reduce the body mass loss during rut, and this may be indicative of active female mate choice of adult males. The dominant males normally form large mobile harems (mating groups), probably as a result of their superior display, fighting, and herding abilities (Skogland 1989). However, the females live in fission–fusion systems and associate normally with various harem-holding males during the rut (Hirotani 1989; Smith et al. 1999). Hence, the females were, to a large extent, able to choose a harem and seemed reluctant to accept the company of only young males especially when adult males are present (i.e., the mixed age group treatments). The young males therefore have to herd intensively to keep astray (from the dominant adult harem holding males) females isolated, as confirmed by the higher frequency of female harassment by the young males compared to the adults in the mixed groups (Fig. 2b). When alone, the young males’ rutting behavior is more clearly expressed (Grønmyr 2004), and the females are probably more receptive to them. Indeed, the frequency of female harassment when exposed to only young males or to a mixture of young and adult males was not significantly different (Fig. 2a). Furthermore, females’ feeding activity was reduced in treatments including both young and adult males as compared to only young males. The same nonsignificant tendency was observed as compared to only adults. Hence, females seem to pay an indirect toll of the increased stress caused by the young males in the mixed treatments by reduced foraging time. Such stress may also induce reduced foraging efficiency, amplifying the reduced energy intake among females. The difference in foraging behavior with male age structure appears, however, minimal.

Young males are sexually inexperienced, and their display seems to be less developed, as also suggested by Clutton-Brock et al. 1982 in red deer and Komers et al. (1999) in fallow deer. Also, their dubious social rank in

relation to females (Kojola and Nieminen 1988) may prolong the courtship phase to overcome female reluctance to mate and, thus, increase the females’ costs. If males’ harassment is costly to females, we may expect a flexible tactic to minimize these costs to evolve. In highly female-biased populations, with few adult males available, female red deer may aggregate in harems (Clutton-Brock et al. 1992) or territories (Carranza and Valencia 1999) held by high-ranked adult males to avoid harassment by subdominants. This accords with the finding of Grønmyr (2004) that guarding by the dominant male within a mating group reduced the frequency of inspection of females and mating attempts by subdominants.

The extreme low male percentages in most of our trials as compared to the situation in the wild (but not necessarily in managed populations) may induce some limitations in the interpretation of our findings. Nevertheless, our findings may have bearings for the management and conservation of ungulate populations and captive or semidomesticated ungulates, where the sex ratio is often highly skewed toward females.

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