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Social rank, feeding and winter weight loss in red deer: any evidence of interference competition?

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Abstract During winter at northern latitudes, large herbivores often exploit patches of concentrated, relatively high quality forage, which may lead to interference competition. The factors affecting success in contests and subsequent dominance rank, such as age and body weight, remain key issues in ungulate behavioural ecology. Maternal effects on offspring body weight are well known, but few studies have investigated if mother's social rank influence offspring rank. Moreover, no study has related dominance rank in ungulates to weight loss during winter. Outcomes of social interactions ($n=7,609$), feeding time and spatial position in red deer (*Cervus elaphus*) hinds and calves, and weight loss of calves, were registered from 1981 to 1996 at six winter-feeding sites within the county of Sør-Trøndelag in Norway. The level of aggressiveness was higher among calves than among adult hinds, and the factors determining the outcome of contests also differed. The initiator won the majority of interactions (more than 90% in both hinds and calves). Social rank was related to both age and body weight in adult hinds, and related to body weight and mother rank in calves. The relationship between feeding time and rank was non-linear. Feeding time was correlated with rank only among high ranked hinds, while there was no such relationship among low ranked hinds or calves. There was no correlation between winter weight loss and social rank in calves. Our study therefore underlines that, although

frequent aggression is observed at artificial feeding sites of northern herbivores, this is not necessarily sufficient to give rise to interference competition.

Keywords Aggression · *Cervus elaphus* · Dominance · Life history · Maternal effects

Introduction

Intra-specific competition for food or other resources occurs either through exploitation or interference (Begon et al. 1996). Exploitative competition is generally regarded as more common than interference competition for large herbivores (e.g. Illius and Gordon 1987), since plant resources are generally of low energetic value per item and widely dispersed so that resource defence is not likely to be a beneficial strategy (Clutton-Brock et al. 1987). A concentration of food resources, however, may lead to increased levels of interference competition in herbivores. This happens frequently during winter at northern latitudes. For example, in marginal habitats in Scandinavia, all marked roe deer (*Capreolus capreolus*) used artificial feeding sites and agricultural areas to some extent during winter, and this was suggested to be critical for their winter survival (Cederlund and Liberg 1995; Holand et al. 1998). Also, high levels of aggression during winter have been reported for northern ungulate populations [roe deer (Espmark 1974); Roosevelt elk (*Cervus elaphus roosevelti*; Weckerly 1999); reindeer (*Rangifer tarandus*; Skogland 1994)].

Aggressive encounters between individuals are inherently costly and dominance hierarchies are often established to minimize the number of energy demanding interactions (Clutton-Brock et al. 1982). Ungulates limit their agonistic interactions to pairwise conflicts (Clutton-Brock et al. 1982), contrary to many primates, where groups of individuals develop patterns of long-term alliances (Cheney and Seyfarth 1990). Escalated interactions may occur more often among individuals close in phenotypic quality and hence social rank, since the

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outcome of fights is less predictable from visual cues, and both individuals invest energy in optimizing their position in the hierarchy (Bernstein 1981).

Fighting ability and dominance in male ungulates are typically related to age and body weight [age (Appleby 1982); age and weight (Clutton-Brock et al. 1982)]. Similarly, social rank of females also correlates with body weight [semidomestic reindeer (Hirotani 1990); bison (*Bison bison*; Lott and Galland 1987)] and age [red deer (*Cervus elaphus*; Clutton-Brock et al. 1982, 1986; Hall 1983; Thouless and Guinness 1986); bighorn sheep (*Ovis canadensis*; Festa-Bianchet 1991)]. However, few studies have assessed the relative influence of both age and body weight on rank and the conclusion from these studies have been conflicting. Both age [red deer (Thouless and Guinness 1986); bison (Rutberg 1986); bighorn (Festa-Bianchet 1991); mountain goat (*Oreamnos americanus*; Côté 2000)] and weight [dairy cattle (*Bos taurus*; Reinhardt and Reinhardt 1975)] have been reported as the main predictor of female social rank. Maternal effect on offspring body weight is well described (e.g. Mech et al. 1991), and is also present in Norwegian red deer (Loison et al., unpublished data), but no study of wild ungulates has investigated whether part of the maternal effect may be caused by correlation in social rank (more than expected based on correlation in body weight).

In many species of ungulates, male fighting ability is correlated with access to females: this includes red deer, where high ranked stags have higher reproductive success than low ranked individuals (Clutton-Brock et al. 1982, 1986). Few studies have identified fitness consequences from rank position among female ungulates, whose reproductive success is limited by their ability to raise offspring (Clutton-Brock et al. 1982). When resources are scarce or vary in quality, high rank may increase foraging time and resource access. High ranked bison cows spent more time foraging than low ranked ones (Rutberg 1986), dominant red deer stags feeding in enclosures acquired better quality pasture and longer grazing bouts than subdominants (Appleby 1980), and bite rate in red deer hinds declined with decreasing distance to a dominant neighbour (Thouless 1990). However, it remains to be determined whether improved foraging conditions for dominant individuals translates to reduced weight loss and risk of starvation during winter compared to low ranked individuals. This is not a trivial question, as dominance may only determine the order in which individual deer feeds, i.e. it may be that subdominant individuals visit artificial foraging sites at times when dominant deer are not present, ingesting the same amount of food as high ranked animals and thus suffering little from low rank.

In western Norway, red deer migrate to coastal, traditional wintering areas, where large numbers of animals aggregate around farmland (Albon and Langvatn 1992). More than 800 red deer have been marked in this area: age is known for most of them. Here, we present an analysis based on 7,609 observations of interactions between adult hinds and between calves at artificial winter feeding sites. We first calculated the level of aggressive-

ness in interactions, since this may indicate to what extent animals compete for a limiting resource. Thereafter we tested whether the level of aggressiveness was dependent on a difference in phenotypic quality (body weight and sex) between interacting individuals, and what factors determined rank in adult hinds (age and weight) and calves (sex, weight and mother's rank). In turn, we tested whether rank is related to time spent grazing and position at feeding site, and to winter weight loss of calves.

Materials and methods

Study area and feeding site

The six feeding sites (Slørdal, Sagøra, Skogan, Mjønes, Heggstad and Venn) were located in Snillfjord municipality in Sør-Trøndelag county (63°30'N, 9°30'E). The topography is rough and varies from sea level to hills, rising to approximately 500 m. The natural vegetation is predominantly open pine forest (*Pinus sylvestris*), with juniper (*Juniperus communis*), heather (*Calluna vulgaris*) and bilberry (*Vaccinium myrtillus*). On flatter ground, the forest has been cleared for agricultural use and is now improved pasture. Snow covers the ground for approximately 4–5 months a year and is usually deep enough to prevent access to grass. Temperatures in mid-winter occasionally fall below –20°C, but may also stay above freezing for similar periods.

The chosen feeding sites were situated in a traditional wintering area where red deer, several years prior to this study, searched for food in the adjacent fields and also used spilled forage from barns. The size of these feeding sites was about 8×10 m and they were shielded from traffic and other disturbances. Hay, and occasionally silage, were used as fodder from January to April. The fodder was evenly distributed within the feeding site. The amount of forage was kept approximately constant and was never super-abundant during this time period. Most deer were observed on the feeding sites Slørdalen and Sagøra, and only on these two sites were we able to establish rank hierarchies.

Study animals and observations

Since 1977, more than 800 red deer have been captured and marked with large numbered ear tags at this location (Albon and Langvatn 1992). Weight, sex and hind leg length was recorded on drugged animals (Loison et al. 1999). Because capture had taken place many years before this study started, most adults present on the feeding site were already marked and of known age.

Behaviour registrations were conducted from 1981 to 1996 on six feeding sites. Observations were made from concealment in a nearby barn at 10–50 m distance, and the animals seemed undisturbed by this activity. Behaviour registrations were not made when darting and marking activity was carried out. To prevent any effects of the drug, we did not register social interactions of individuals which had been immobilized the same day.

Aggressiveness

Aggressiveness was categorized into two levels. Level 1 consisted of threatening behaviour like nose and ear threats and displacements by walking straight towards another animal, usually with the head held high. Level 2 (hereafter termed 'escalated fights') consisted of both threats and physical attacks like biting, butting, kicking (usually with a single foreleg) or boxing (when one or both animals in an interaction pair reared on their hind legs and slapped at the other).

Table 1 Number of individuals (*n*), total number of interactions (*Int.*), and the percentage of potential dyads included in social rank analyses of red deer hinds and calves. Note that the data used in analyses of social rank was only a subset of the full dataset of outcome of red deer interactions (see Material and methods)

Year	Feeding site	Hinds			Calves		
		<i>n</i>	Int.	Dyads (%)	<i>n</i>	Int.	Dyads (%)
1986	Slørdalen	22	658	68.2			
1987	Slørdalen	20	580	67.4	8	84	71.4
1987	Sagøra	14	562	81.3	5	26	80.0
1988	Slørdalen	18	623	70.3	6	46	86.7
1994	Slørdalen	18	408	62.7	8	86	71.4
1995	Slørdalen	33	1904	69.9	16	464	81.7
1996	Slørdalen	9	86	75.0	10	140	73.3

Outcome of fights

We observed 6,629 interactions involving two adult hinds (≥ 1 year) and 980 interactions involving two calves. In each case, we identified the initiator of the interaction, and subsequently which of the individuals won and lost (the winner physically displaced the loser).

Social rank

We calculated social rank based on outcome of fights only for individuals with known age and weight (reducing the number of interactions to 652 for hinds and 974 for calves). We established rank among animals regularly present on the two feeding sites Slørdalen (1986–1988) and Sagøra (1987), where the majority of agonistic interactions were observed (Table 1).

Estimation of dominance in previous studies has been conducted in various ways (e.g. Clutton-Brock et al. 1979; Barrette and Vandal 1986; Rutberg 1986) and bias due to the influence of individual propensities to fight and to systematically select for opponents have been questioned (Freeman et al. 1992). An argument against such methods is that a variety of patterns of agonistic rates may occur within the framework of a dominance hierarchy (Fairbanks 1994). We calculated social rank according to the method used in Barrette and Vandal (1986), because this method makes no assumption of dominance transitivity.

$$\text{Rank} = (\text{Wins}+1) / (\text{Losses}+1)$$

The individual with the highest ratio was ranked as number one. Separate analyses were conducted for each year, feeding site and age segment (hind or calf). This procedure treats each individual with respect to the rest of the group simultaneously and not just one dyad at a time. Therefore, it gives an individual's overall standing in the group, which is what its rank is supposed to mean.

Many of the observed interactions involve individuals that were rarely observed and for which rank cannot be calculated. To avoid a large number of missing dyads, we used the criterion that every ranked animal should have interacted with at least 50% of the other ranked animals in the same category (hinds or calves). The exclusion process was conducted in the following way:

1. The individual which had interacted with the lowest number of individuals of its own category (regardless of number of interactions) was identified
2. All interactions involving this individual were excluded from the data set
3. This process continued until all remaining individuals had interacted with at least 50% of the other individuals left in the data set. Individuals with the same win/loss ratio (with a difference < 0.001) were assigned equal rank.

We acknowledge that this exclusion process may deselect the individuals less prone to initiate fights, which may well be related to the position in the hierarchy (i.e. on the very top or the very bottom).

Relative rank

The number of individuals ranked for each site and year varied greatly. To compare rank across sites and years, we calculated a measure of relative rank. This is acquired by dividing the rank of the individual by the total number of ranked individuals within the feeding site and year. The result from this calculation is subtracted from 1, giving a number ranging from 0 to close to 1, with the highest ranked animals attaining the highest values.

$$\text{Relative rank} = 1 - \text{Rank} / \text{Number of ranked individuals}$$

This measure closely corresponds to dominance value (Eccles and Shackleton 1986) which is calculated for each individual as the proportion of opponents dominated.

Body weight

Hinds were weighed during the first week of April. The calves were weighed in early winter and re-weighed during late winter so that weight loss could be estimated. We used the difference between first and latest weighing as a response, and also entered the number of days and date of first weighing as covariates, in addition to factors that we are interested in.

Mother-calf pairs

Mother-calf associations were identified based on activities such as grooming, licking, suckling, close standing and temporal pattern of appearance on feeding site.

Feeding time

Focal individuals were intensely observed during feeding bouts of 5 minutes. Number and duration of feeding breaks were recorded, and subtracted from the total observation period in order to get an estimate of efficient feeding time. No more than three feeding observations were recorded in 1 day for each animal.

Feeding zone

Hay was evenly distributed all over the predefined (8×10 m) feeding area. The site was divided into a central, intermediate and peripheral feeding zone depending on distance from the centre of the feeding site. Feeding zones did not differ systematically according to the amount of available food.

Statistical analyses

To test for possible non-linear relationships between response variables and predictor variables in non-nested models, we fitted generalized additive models (GAM) using smoothing splines (Hastie and Tibshirani 1990; Venables and Ripley 1999). The complexity of the curve, i.e. the number of degrees of freedom associated with the smoothing spline, was selected by repeated fitting of the GAM. We fitted the model with varying df_{spline} for one variable (1–5) while holding df_{spline} of the other variables constant. We then tested the fit of the different models in an ANOVA setting (Venables and Ripley 1999). Linearity of nested models (models including random

factors) was evaluated by checking residual plots of fitted models. In case of deviation from linearity, adequate transformations (e.g. natural logarithm and arcsine) were tested. If the relationship was still non-linear, the data set was split and linear modelling was conducted on subsets.

Three different categories of linear statistical models were used. Generalized linear models (GLM; see Venables and Ripley 1999) were used in non-nested analyses of body weight loss of calves during winter and relationship between mothers and calves social ranks. Linear mixed-effects models (LME; see Venables and Ripley 1999) were used in nested analyses when the response variable was continuous and assumed to be normally distributed. This was the case in analyses of the relationship between relative rank in hinds and calves (which were predictors) on proportion of time spent feeding (continuous response variable, nested on the level of individuals). Finally, generalized linear mixed models (GLMM; Lindsey 1999) were used in nested analyses where the response variable was expected to be either binomially or Poisson distributed. GLMM was used to analyse what determines outcome of fights (nested on the level of interacting pair of individuals). We entered age and weight difference between aggressor and victim in this model. Age and weight difference could take negative values (if the aggressor was younger and lighter than the victim, respectively). As prime-aged individuals may have higher rank than older individuals, we also calculated age difference relative to distance to prime age (10 years old as break point). We also used GLMM to analyse what determines the number of feeding breaks (nested on the level of individuals). The effect of interactions of two continuous variables was analysed by using the product of the two standardized variables as a separate term.

We used a combination of direct hypothesis testing and model selection. The reason for relying on model selection was the fairly large number of parameters in some cases for which there was not always a clear prediction (but see predictions for most factors in Introduction). When using model selection, we used the Akaike information criterion (AIC; Akaike 1974), which is calculated as the deviance plus twice the number of estimable parameters of a model (Burnham and Anderson 1998). This criterion allowed us to select the most parsimonious model, i.e. the "best" balance between explained variance and degrees of freedom. We considered that two models differing in AIC value by more than 1 were significantly different (Ims and Yoccoz 1997). In GLM and LME models, the best model was found by using the stepwise AIC function, automatically finding the model with the lowest AIC value. In GLMM models, the best models were found manually following the same procedure as the step AIC by starting with the full model and successively removing the terms which decreased the AIC value most.

For inference, we considered whether a predictor variable was selected in the most parsimonious model, and we also analysed magnitude, direction and precision of all predictor variables through *t*-tests and *F*-tests. All models were checked for assumptions of

linearity, and statistically defined influence values (Cook's *D*; Venables and Ripley 1999).

GAM, GLM and LME were conducted in S-plus (Insightful, Seattle, Wash., USA), whereas GLMM was conducted in R (<http://www.r-project.org>).

Results

Level of aggressiveness

Interaction frequency of individual focal red deer was overall high, and tended to be higher in hinds (mean=3.26 interactions/5 min, SE=0.16, $n=175$) than in calves (mean=2.92 interactions/5 min, SE=0.17, $n=153$; GLMM: $z=1.73$, $df=327$, $P=0.083$). A total of 39.6% of interactions were escalated fights. Escalated fights were more common in calf (56.0%, $n=979$) than in hind interactions (37.1%, $n=6,628$).

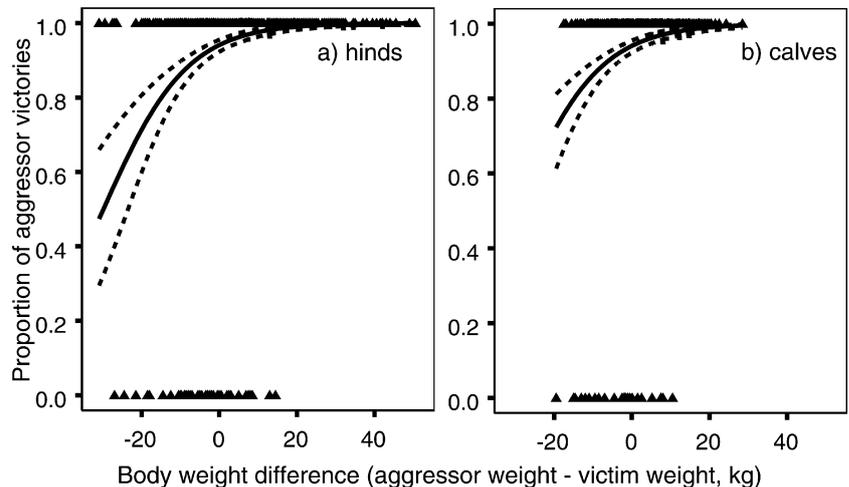
In hinds, the level of aggressiveness was not dependent on the difference in body weight between contesting individuals (mean=-0.0519, SE=0.0902; GLMM: $z=-0.58$, $df=1,084$, $P=0.565$).

In calves, escalated fights were more common when individuals with similar body weight were interacting (GLMM: $z=-2.21$, $df=970$, $P=0.027$). 63% of interactions were escalated fights when competitors were of similar weight, compared to only 53% when the weight difference was 10 kg. There was no effect of aggressor sex on level of aggressiveness (mean=0.271, SE=0.231; GLMM: $z=1.18$, $df=972$, $P=0.240$).

Determining factors of fighting success and rank in hinds

The aggressor won a large majority of fights (96.6%, $n=6,629$), and the success of the aggressor increased as the winter progressed (GLMM: $z=2.25$, $df=651$, $P=0.025$). When the phenotypic quality of the aggressor and the victim were equal, aggressors won 92.2% of fights on 10 January (day 10) and 99.4% on 10 April (day 100). The

Fig. 1 Absolute body weight difference (aggressor weight – victim weight in kg) in red deer and the likelihood for **a** hind aggressors and **b** calf aggressors to win interactions (the *dashed lines* represent upper and lower standard errors of the predicted value). Data points are presented as *triangles* (aggressor victory = 1, aggressor loss = 0)



aggressor was more likely to win an interaction if it was heavier than the victim (mean=6.106, SE=2.236; GLMM: $z=2.731$, $df=651$, $P=0.006$; Fig. 1a), and also when it was closer to prime age than the victim (mean=-0.154, SE=0.077; $z=-2.012$, $P=0.044$). In a sample, which did not include very old females, for which both age and weight was available ($n=34$), social rank (which is a direct derivative of the outcome of fights) was related to both age (Fig. 2; mean=0.031, SE=0.012; $t=2.642$, $P=0.013$) and weight (mean=1.148, SE=0.354; $t=3.247$, $P=0.003$), while the interaction was not significant when added to the model (mean=0.108, SE=0.105; $t=1.027$, $P=0.313$). In a larger sample ($n=114$) for which we had age but not weight, both age (mean=0.129, SE=0.017; $t=7.737$, $P<0.001$) and age² (mean=-0.006, SE=0.001; $t=-5.914$, $P<0.001$) were significant predictors of rank, with a peak in rank around 10 years of age.

Determining factors of fighting success and rank in calves

The aggressor won the large majority of fights (96.9%, $n=973$) and the success of the aggressor increased as the

winter progressed also for calves (GLMM: $z=2.41$, $df=972$, $P=0.016$). When the body weights of the aggressor and the victim were equal, aggressors won 90.2% of fights on 10 January (day 10) and 98.8% on 10 April (day 100). The aggressor was more likely to win an interaction if it was heavier than the victim (GLMM: $z=4.54$, $df=972$, $P<0.001$; Fig. 1b) and hence body weight influenced social rank (Fig. 2b). Since body weight of male calves was higher (51.8 ± 1.12 kg; $n=29$) than for female calves (49.1 ± 1.01 kg; $n=24$), the median relative rank of males was significantly higher than that of female calves (males 0.500, females 0.275; Wilcoxon rank-sum test: $z=1.97$, $P=0.049$). Sex did not enter the final model, indicating that the effect of sex on calf rank was caused by male calves being heavier than female calves.

In the total sample of ranked red deer, 23 mother-calf pairs were known. Median relative rank of mothers with male calves (0.606, $n=11$) did not differ significantly from mothers with female offspring (median relative rank 0.472, $n=12$; Wilcoxon rank-sum test: $z=0.800$; $P=0.424$). Mother and calf body weight were relatively weakly correlated ($r=0.229$). Two models of calf rank were regarded as equally good based on AIC, one containing only calf weight (AIC=-63.5, $R^2=0.38$), the other including calf weight and rank of mother (AIC=-63.7, $R^2=0.44$). Entered in the same model (ANOVA, $n=23$), both mother rank ($F_{1,20}=4.94$, $P=0.038$) and calf body weight ($F_{1,20}=10.60$, $P=0.004$) correlated positively with calf rank. We therefore found a marginal effect of mother rank on calf rank after the effect of calf body weight was accounted for (Fig. 3).

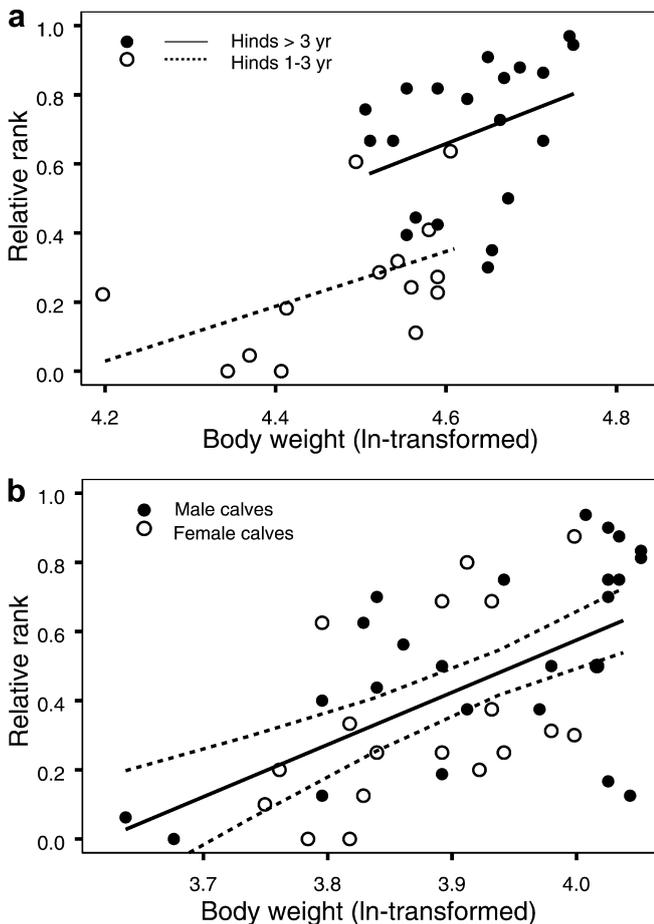


Fig. 2 Influence of body weight (ln-transformed) on relative rank in red deer: **a** subadult and adult hinds and **b** calves. No very old females were included in this analysis

Social rank and feeding time

Feeding time in adult hinds was non-linearly related to relative rank (GAM analyses). Based on this, hinds were divided into low (relative rank <0.6) and high (≥ 0.6) ranked hinds prior to LME analyses. In low ranked hinds, relative rank did not influence the proportion of time spent feeding (Table 2). Only among top ranked individuals was

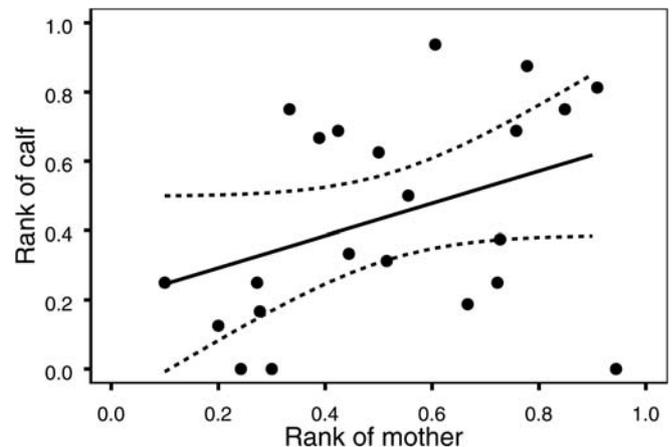


Fig. 3 Correlation between relative rank of red deer mothers and calves (dashed lines 95% confidence interval)

Table 2 Relationship between proportion of time spent feeding, relative rank and individual aggressiveness (the proportion of fights initiated by the individual that was escalated) in high- (relative rank ≥ 0.6) and low-ranked hinds (relative rank < 0.6). These two groups were selected based on GAM analyses so that relationships between feeding time and rank were linear within the two groups. Values of relative rank and individual aggressiveness were arcsine-square root transformed. The analysis was nested at the level of individual

	LME estimate	SE	df	t	P
High-ranked hinds					
Intercept	0.811	0.224	94	3.61	0.0005
Date	0.00437	0.00161	94	2.72	0.0077
Relative rank (arcsine)	0.576	0.212	14	2.72	0.0167
Individual aggressiveness (arcsine)	-1.14	0.2951	14	-3.86	0.0017
Relative rank \times aggressiveness	0.212	0.0729	14	2.91	0.0113
Low-ranked hinds					
Intercept	0.893	0.256	70	3.50	0.0008
Date	0.00709	0.00199	70	3.56	0.0007
Relative rank (arcsine)	0.122	0.244	17	0.498	0.6251
Individual aggressiveness (arcsine)	-0.611	0.439	17	-1.39	0.1824
Relative rank \times aggressiveness	-0.0169	0.0836	17	-0.202	0.8421

there a positive relationship between rank and feeding time (Table 2). This was due to a lower number of feeding breaks: females with relative rank 0.6 had 4.3 feeding breaks/5 min observation period, while a female with relative rank 0.9 had 2.6 feeding breaks/5 min observation period (GLMM: $z = -2.96$, $df = 88$, $P = 0.031$).

In calves, rank did not influence the proportion of time spent feeding (LME: $n = 153$, $df = 14$, $t = 0.15$, $P = 0.881$). There were no sex differences in feeding time (LME: $n = 153$, $df = 14$, $t = 1.22$, $P = 0.244$).

Spatial feeding position

Spatial position on the feeding site was not related to rank in hinds (ANOVA: $F_{2,108} = 2.31$, $P = 0.100$; central zones: mean rank = 0.63, SE = 0.03; intermediate zones: mean rank = 0.65, SE = 0.03; peripheral zones: mean rank = 0.72, SE = 0.03), although the proportion of time spent feeding differed between spatial feeding zones (ANOVA: $F_{2,117} = 7.39$, $P < 0.001$). Hinds used less time feeding in the most peripheral zone (mean = 0.80, SE = 0.04) than in the intermediate (mean = 0.90, SE = 0.01) and central zones (mean = 0.91, SE = 0.01).

The average rank of calves differed between spatial feeding zones (ANOVA: $F_{2,150} = 10.5$, $P < 0.001$). High ranked calves were more frequently observed in central zones (mean relative rank = 0.60, SE = 0.04) than in intermediate zones (mean relative rank = 0.48, SE = 0.05) and least in peripheral zones (mean relative rank = 0.40, SE = 0.03). Possibly because of this, interruption frequency increased with rank; calves of rank 0.1 were disturbed 2.5 times while calves of rank 0.9 were disturbed 3.5 times per 5 min observation period (GLMM: $z = 2.55$, $df = 152$, $P = 0.011$) and there was no clear relationship between feeding time and feeding zone (ANOVA: $F_{2,150} = 2.71$, $P = 0.070$). There were no sex differences in use of feeding zones (GLM: $t = -1.18$, $df = 152$, $P = 0.120$).

Social rank and body weight loss in calves

Winter weight loss in calves ($n = 48$) ranged from 0 to 12 kg (0 to 24% of January weight), while daily weight loss rate varied from 0 to 0.19 kg. Social rank was not included in the most parsimonious model of weight loss (AIC selected model = 42.6; including social rank: AIC = 44.1), and there was no correlation between rank and weight loss when tested directly (GLM: $t = -0.08$, $df = 41$, $P = 0.935$). Year ($F_{4,33} = 14.7$, $P < 0.001$), date of initial weighing ($F_{1,33} = 56.5$, $P < 0.001$) and initial body weight ($F_{1,33} = 16.0$, $P < 0.001$) explained most of the weight loss in calves ($R^2 = 0.74$). We found that large calves lost more weight on an absolute scale. On a relative scale, however, weight loss was independent of initial weight (see Loison et al. 1999). We controlled for number of days between weighings. As these data are part of a larger dataset that has been analysed elsewhere for other covariates (Loison et al. 1999), we refer to this study for other factors affecting weight loss during winter.

Discussion

Our study provides additional evidence for high levels of aggression in northern cervid populations during winter (Espmark 1974; Skogland 1994; Weckerly 1999). In red deer, this is typically more pronounced at artificial feeding sites (Hall 1983) than in natural habitats (Clutton-Brock et al. 1986). Our study is the first to relate social dominance rank to weight loss and therefore prospects for survival, but we failed to find such a correlation, raising doubts about earlier claims of interference competition in cervids during winter.

Dominance hierarchies

Individuals may be expected to interact more often and more intensely with animals of similar status [Bernstein 1981; New Forest ponies (*Equus caballus*; Tyler 1972); diary cattle (Brantas 1968; Reinhardt and Reinhardt 1975)], but this has not always been found [red deer

(Appleby 1983); Nubian ibex (*Capra ibex nubiana*; Greenberg-Cohen et al. 1994)]. In our study, the level of aggressiveness was higher among red deer calves ranked as neighbours in the hierarchy, but such a relationship was not found in hinds. For both calves and hinds, the aggressor won a large majority of the interactions [see also: red deer (Thouless and Guinness 1986); Roosevelt elk (Weckerly 1999); bighorn sheep (Eccles and Shackleton 1986); pronghorn (*Antilocapra americana*; Fairbanks 1994)]. Social rank was therefore primarily maintained by dominant individuals initiating fights after using one or more visual cues (most likely body weight in these antlerless age-sex groups) to assess that they were likely to win. The aggressors also won fights quite often when they were inferior in terms of phenotypic quality measured as body weight or age (Figs. 1, 2). This indicates that factors other than age and body weight are of importance for the outcome of contests.

Rank among adult hinds – age and/or weight?

Age and weight are closely correlated in ungulates (e.g. Mysterud et al. 2001), and the relative roles for social rank are therefore difficult to disentangle. In a group of fully-grown bison cows with low variation in body weight, age was the best predictor of social rank (Rutberg 1986). Possibly, age is more important than weight where dominance relationships remain stable for a long time (Thouless and Guinness 1986). Other studies, which have included a larger proportion of young individuals, found that both age and weight strongly correlated with rank (Schein and Fohrman 1955), or that weight was a better predictor than age (Reinhardt and Reinhardt 1975). Social rank among the hinds in our study was related both to age and body weight.

Calf rank – weight and/or mother's rank?

Body weight difference was the predictor corresponding most closely with the outcome of fights in calves (see also Suttie 1983). Calf birth weight and early development are positively correlated to maternal physical conditions (Clutton-Brock et al. 1982; Lenvik et al. 1988), so-called maternal effects (e.g. Mech et al. 1991). In mouflon sheep (*Ovis gmelini*), a positive correlation has been found between the rank of mothers and calves and yearling offspring (Guilhem et al. 2002), but body weight was not controlled for. Strong maternal effects in body weight have recently been found for the same population that we study (Loison et al., unpublished data). We provide evidence here that the rank of mother and calf is correlated even after the effect of body weight is adjusted for.

Rank and feeding time

Access to limited food resources has been found to correlate positively with social rank in most studies (e.g. Appleby 1980; Barrette and Vandal 1986; Masteller and Bailey 1988, but see Eccles and Shackleton 1986). Promoted feeding efficiency for high ranked individuals has also been reported for free ranging animals where the resource was not limited (Lovari and Rosto 1985; Rutberg 1986; Thouless 1990). No earlier studies have tested whether the relationship between rank and feeding time may be non-linear. In our study, rank was correlated with an increase in feeding time only among superior adult hinds. In our study, inferior deer were not physically prevented from access to the feeding site, and the reason for higher feeding time in high ranked hinds was due to more efficient feeding associated with lower number of feeding breaks.

Spatial position in the herd

Hamilton (1971) predicted that low ranked individuals should mainly be found at the boundaries of social units. This was found for red deer stags feeding on a Scottish winter feeding site (Schmidt and Hoi 1999). Low ranked calves in this study used the peripheral parts of the feeding sites more often than high ranked individuals. However, spatial position at feeding sites did not depend on rank in adult female hinds in our study. Forage was evenly distributed at the feeding sites, and spatial distribution on the feeding site was of minor importance in determining proportion of time spent feeding. High ranked calves did not use their hierarchical position to obtain a higher efficient feeding time than inferior calves in the periphery of the feeding site. Instead, they entered central parts of the feeding site and were interrupted by foraging adult animals, leading to more feeding breaks than for the low ranked individuals. Inferior and superior calves nevertheless ended up with the same efficient foraging time, indicating that the duration of feeding breaks in high ranked calves were shorter than for low ranked calves.

Rank, feeding time, weight loss and interference competition

A necessary final step to show that interference competition occurs at feeding sites is that aggressive encounters observed, and the rank obtained, have consequences for individuals in terms of weight loss and therefore prospects for survival. However, winter weight loss of calves was not related to individual rank, and there was hence no evidence that interference competition did occur. On a larger dataset, including 204 calves, relative weight loss was not dependent on body size (Loison et al. 1999). Given the close correlation between calf weight and rank, our result is probably therefore robust. This is also supported by the lack of a relationship between rank and

feeding time in calves. Indeed, as rank and feeding time was only correlated among top-ranked hinds, we can conclude that interference competition at artificial feeding sites is probably not an important mechanism for population dynamics.

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