Social rank and winter forage quality affect aggressiveness in white-tailed deer fawns

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Achieving a high social rank may be advantageous for individuals at high population densities, because dominance status may determine the priority of access to limited resources and reduce individual loss of body mass. The establishment of dominance relationships between individuals involves variable levels of aggressiveness that can be influenced by resource availability. The relationship between social rank and aggressiveness and the impacts of resource abundance on aggressiveness are, however, poorly understood, but may be relevant to understand the mechanisms determining dominance relationships between individuals. We experimentally simulated, in seminatural enclosures, a deterioration of winter forage quality induced by a high-density deer population and examined the effects of (1) social dominance and (2) diet quality on aggressiveness, forage intake and body mass loss of white-tailed deer, *Odocoileus virginianus*, fawns during two winters. Within diet-quality treatments, fawns were consistently organized into linear hierarchies and showed clear dominance relationships. Dominants initiated more interactions and showed higher aggressiveness than subordinates, but subordinates had higher forage intake than dominants throughout winter. Social rank did not influence cumulative body mass loss of fawns. During both winters, fawns fed the control diet maintained their aggressiveness level, whereas fawns fed the poor-quality diet decreased it. Our experimental approach revealed that white-tailed deer responded to a reduction in winter forage quality by modifying their aggressiveness, indicating that ungulates may show plasticity not only in their foraging behaviour in response to decreased resources but also in their social behaviour.

Several gregarious mammals are organized in stable and linear social hierarchies (Thompson 1993; van Noordwijk & van Schaik 1999; Côté 2000a; Veiberg et al. 2004). The establishment of dominance relationships between individuals usually involves the use of aggressive behaviours, which can be modulated both by the value of the contested resource and by changes in body condition of individuals (Appleby 1980; Rutberg 1986; van Schaik 1989; Grenier et al. 1999). High dominance status or social rank may be advantageous when competition for limited resources is intense (Appleby 1980; Gouzoules et al. 1982; Barrette & Vandal 1986). The relation between dominance status and aggressiveness, however, is not constant

across studies and has been poorly documented during periods of high density and/or resource shortages. The study of this relationship may be relevant to understand the mechanisms determining dominance relationships between pairs of individuals (Maynard Smith 1974; Rutberg 1986) and to assess the general implications of behavioural changes in response to reduced forage quality or high population density.

During interactions involving access to resources, individuals may show variable levels of aggressiveness (Ozoga 1972; Weckerly 2001). Aggressive encounters between individuals are inherently costly, so aggressiveness may depend on the value of the contested resource (Grenier et al. 1999; Barroso et al. 2000; Koenig et al. 2004). The relation between social rank and aggressiveness, however, is not straightforward. High aggressiveness is likely to increase the chance of winning an encounter,

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so aggressiveness and social rank may be positively related (Thompson 1993; Araba & Crowell-Davis 1994; Barroso et al. 2000). However, a high social rank is not necessarily associated with high aggressiveness, because dominant individuals may need to defend their position only against those ranked immediately below them in the hierarchy, not against those several ranks away, thus reducing the number of interactions (Hall 1983; Fairbanks 1994; Côté 2000a). Social dominance may also contribute to a stable social environment, where aggressiveness and the energy costs and risk of injury associated with fighting are reduced (Maynard Smith 1974; Clutton-Brock et al. 1979; Hand 1986). The level of aggressiveness, the stability of dominance relationships and the correlation between social rank and aggressiveness could thus be interpreted by considering the ratio of fighting costs to benefits potentially conferred by a contested resource (Maynard Smith 1974; Clutton-Brock et al. 1979; Rutberg 1986).

Within groups, social rank may determine an individual's priority of access to resources (Appleby 1980; Barrette & Vandal 1986) and can therefore be critical during competition for limited feeding sites, bedding sites or mates. Access to limited food resources (Barrette & Vandal 1986; Eccles & Shackleton 1986; Masteller & Bailey 1988) and feeding efficiency (Lovari & Rosto 1985; Rutberg 1986; Thouless 1990) may be positively correlated with social rank in ungulates. Hence, a high social rank may be a great advantage for individuals in situations where competition is intense or resources are scarce, such as at high population density or during food shortages (Clutton-Brock et al. 1986; Albon et al. 1992).

The recent increases in the density of several ungulate populations in temperate regions have resulted in negative impacts on the abundance and the quality of forage resources (Côté et al. 2004). Moreover, during winter, wild northern ungulates have to deal with low forage abundance (Gray & Servello 1995; Tremblay et al. 2005) and high energy expenditures caused by the demands for thermoregulation and locomotion in deep snow (Moen 1976). Winter forage is generally limited compared to summer forage (Verme & Ullrey 1972; Gray & Servello 1995), and the low quality of available browse is insufficient to support the nutritional and energetic needs of herbivores (Robbins 1993). These constraints may increase the importance of social dominance for priority of access to limited resources and, eventually, for individual winter survival. By increasing access to forage, a high social rank may result in improved body condition and survival (Espmark 1974; Kojola 1997).

Low forage abundance and quality may also influence aggressiveness in wild ungulates. Appleby (1980) observed an increase in the rate of interactions with decreasing forage conditions across seasons in red deer, Cervus elaphus. High levels of aggressiveness during winter have also been reported in many northern ungulate populations, especially at supplemental feeding sites (Espmark 1974; Grenier et al. 1999; Weckerly 1999). Other studies have reported an increase in the frequency but a decrease in the intensity of aggressive behaviours throughout winter (Ozoga 1972; Hall 1983; Barrette & Vandal 1986). The effects of reduced forage conditions during winter on aggressiveness, however, are poorly understood and may be related to variations in body condition, especially at high population density.

On Anticosti Island, Québec, Canada, severe negative effects of browsing by introduced and abundant white-tailed deer, Odocoileus virginianus, were observed on boreal forest composition (Potvin et al. 2003; Tremblay et al. 2005). Preferred winter forage (deciduous browse) was almost completely eradicated before the 1930s, and the current alternative preferred forage in winter is balsam fir, Abies balsamea (Potvin et al. 2003). Deer diet is completed by white spruce, Picea glauca (20%) and lichens (10%) (Lefort 2002). White spruce stands are rapidly replacing balsam fir stands on the island and, therefore, deer are likely to include a higher proportion of white spruce in their diet in the near future, although white spruce is normally avoided by deer (Halls 1984; Sauvé & Côté 2007). White spruce is a lower-quality forage than fir because it contains greater concentrations of fibres and tannins (Sauvé & Côté 2007), but it is the only alternative browse species available on Anticosti Island (Tremblay et al. 2005). A diet containing a higher proportion of white spruce would therefore be of lower quality than the current diet based on fir (Sauvé & Côté 2007) and could have detrimental effects on several behavioural parameters and life-history traits of deer such as aggressiveness, forage intake and body mass loss. Moreover, a high social rank may become more important when diet quality is reduced.

Here, we experimentally simulated the long-term deterioration of winter forage quality caused by a high-density deer population and examined the effects of social dominance on (1) aggressiveness, (2) forage intake and (3) body mass loss of captive white-tailed deer fawns fed two diet qualities. A companion study (Taillon et al. 2006) revealed that fawns fed on a poor-quality diet maintained higher forage intake throughout the winter than fawns fed a control diet, suggesting a compensatory response to the decrease of forage quality. Body mass loss of fawns over the winter, however, was not affected by diet quality. Our previous study did not assess the effects of social rank. Within diet-quality treatments, we predicted that dominant deer would be more aggressive when competing for access to resources, have a higher forage intake and, consequently, show lower body mass loss during winter than subordinates. We predicted that social rank would have greater effects when resources were the most limited (i.e. when forage quality was low: contained a high proportion of white spruce). We also predicted that aggressiveness of all individuals would decrease during winter because all individuals would have less energy to allocate to aggressive behaviour following body mass loss.

METHODS

Study Area

Anticosti is a 7943-km^2 island in the Gulf of St Lawrence, Québec, Canada. The sub-boreal climate is characterized by cool summers and long winters (Huot 1982).

The dominant tree species in the boreal forests of the island are white spruce, balsam fir and black spruce, *Picea mariana* (Potvin et al. 2003). There were no indigenous large herbivores on the island before the introduction of 220 white-tailed deer in the late 1800s (Côté 2005). In the absence of natural predators, the population increased rapidly soon after introduction. The white-tailed deer population of Anticosti is at the northern fringe of the species' distribution, and local densities reach more than 20 deer/km^2 (Potvin & Breton 2005). The high density of deer has significantly affected the native flora, mainly herb and shrub layers, of the island (Potvin et al. 2003). Moreover, because of overbrowsing by deer, almost no balsam fir stands have regenerated since the 1930s (Potvin et al. 2003). Within the next 50 years, most of the balsam fir stands are expected to disappear from the island and to be replaced by white spruce stands (Potvin et al. 2003).

Captures

We captured 26 white-tailed deer fawns (6−7 months old) in late autumn 2002 ($N = 13$) and 2003 ($N = 13$) in the western part of Anticosti Island. Only fawns were captured because they represent the most vulnerable segment of the population to winter conditions (Dumont et al. 2000), and because forage quality during the first winter of life can have long-term effects on body condition and life-history traits (Solberg & Sæther 1994; Stewart et al. 1999). We physically restrained deer using Stephenson box traps, drop-nets, net guns or canon-nets (Haulton et al. 2001) baited with balsam fir and commercial cow feed (Shur-Gaint prepartum cow feed, Agribrands, Purina Canada Inc., St Hubert, Québec, Canada). We also used chemical immobilization with a mixture of Telazol (200 mg/ml; Fort Dodge Animal Health, Fort Dodge, Iowa, U.S.A.) and xylazine (100 mg/ml; Bimeda-MTC Animal Health Inc., Cambridge, Ontario, Canada) at doses of 6 mg/kg and 3 mg/kg, respectively, administered remotely with a rifle and radiotransmitter-equipped darts (Pneu-Dart Inc., Williamsport, Pennsylvania, U.S.A.; Miller et al. 2003). We used yohimbine (2 mg/ml; Lloyd Laboratories, Shenandoah, Iowa, U.S.A.) as an antagonist for xylazine (Wallingford et al. 1996). We individually marked all fawns with plastic eartags (4-cm diameter; Allfex, medium size, Brussels Agri Services Ltd, Brussels, Ontario) and relocated them to an outdoor enclosure usually within 30 min of capture.

Experimental Design

We established an 80 × 150-m enclosure surrounded by a 4-m-high game fence in a mature white spruce stand, where none of the trees had branches lower than 3 m, the shrub layer was absent and litterfall of spruce twigs and lichens were negligible. The enclosure was further subdivided into two sections of 80 × 50 m, each with 30−40% of the initial forest maintained as cover. Three basic wood shelters were built in each section to simulate wind-protected areas in the natural forest.

At the beginning of January each year, fawns were divided into similar groups based on sex and body mass.

In 2003, the control group included five males and two females, and the poor-quality diet group included four males and two females. In 2004, the control group included two males and five females and the poor-quality diet group included three males and three females. There was no sexual dimorphism and no significant difference in initial mean ± SE body mass between the two groups of fawns in 2003 (control diet: 28.2 ± 1.8 kg; poor diet: 28.8 ± 1.9 kg; paired *t* test: $t_{1,12} = -0.24$, $P = 0.81$) and 2004 (control diet: 26.9 ± 1.2 kg; poor diet: 26.4 ± 1.3 kg; $t_{1,11} = 0.24$, $P = 0.81$).

The experimental diets were composed of a combination of white spruce and a mixture of balsam fir and arboreal lichens that grow on fir branches, in different proportions of fresh weight. The control diet represented the actual winter diet composition of free-ranging deer on Anticosti (i.e. 70% balsam fir, 20% white spruce and 10% lichens; Huot 1982; Lefort 2002). The poor diet was 50% fir, 40% spruce and 10% lichens. Fir (with lichens) and spruce were harvested near the enclosure and shredded separately in a wood chipper (Yard Machines-5 HP wood chipper). This created a uniform mixture, which prevented fawns from selecting one of the diet components. Using micro-histological analyses of faeces, we verified that fawns ate the proportion of spruce and fir that we offered them (see Taillon et al. 2006). Each fawn received 2 kg of fresh food daily, an amount considered sufficient to meet the basic metabolic needs of a 30-kg fawn (Huot 1982). Fawns were considered to be limited only by the quality and not by the quantity of forage, because there was always food left in the feeding troughs. Water was accessible at all times as snow.

Monitoring

We generally observed the two sections of the enclosure simultaneously for approximately 6 h each day. From January to mid-February, observations were made during the complete daylight period (i.e. 0830−1530 hours). From mid-February to mid-April, observations were conducted alternatively in the morning (sunrise to 1200 hours) and the afternoon (1200 hours to sunset) to encompass the total daylight period. We performed 43 observation periods for the control diet group and 45 observation periods for the poor diet group in 2003 and 53 observation periods per enclosure in 2004 (total observation time was 707 h in 2003 and 616 h in 2004).

We used spotting scopes (15−25×) and binoculars (8 × 42) to conduct behavioural observations from elevated blinds situated at 15 m from the enclosure fence. We determined the social hierarchy of experimental groups from 17 January to 18 April in 2003 and from 14 January to 27 March in 2004. We used ad libitum sampling and focal observations (Altmann 1974) to record aggressive interactions occuring at the food source, at bedding sites, on trails and at the weighing scale. Initiator, winner and loser were noted for each interaction (Hand 1986). Aggressive behaviours included Ear drop-hard look (ears along the neck and intent stare), Kick (strike with one front foot), Chase (charge and pursuit) and Flail

(strike with both front feet) (Ozoga 1972). The main submissive behaviour was Avoidance, when an individual avoided a possible opponent by walking away. In each section of the enclosure, food was provided in a single feeding trough (2.5 m × 30 cm × 30 cm). The trough was placed at the forest edge and was large enough to allow access to food by all individuals simultaneously. Every day, we observed dominant and subordinate fawns feeding at the same time at the trough. This set-up favoured agonistic interactions without limiting individual access to food or impairing the ability of individuals to recognize each other, which has been shown to generate inconsistencies in dominance relationships (Côté 2000b).

To determine the aggressiveness of individuals, we performed a 1-h focal observation on each fawn almost daily and noted all aggressive interactions between the focal animal and all other fawns occuring during the focal period. We also noted all opportunities of interactions. Opportunities were defined as all situations where an individual was seen within 4 m of the focal individual, regardless of whether an interaction occurred (Côté 2000a). Focal observations during which no opportunity of interaction occurred were excluded. We divided the number of interactions initiated by the focal individual by the total number of opportunities for interactions. This allowed us to take into account the variation in the number of opportunities for interactions occurring between focal observations and gave a measure of aggressiveness (from 0 to 1) independent of group size (Côté 2000a). All observations were conducted by two observers trained together.

We measured body mass (±0.5 kg) at least once a week for most individuals using an electronic platform scale baited with less than 100 g of commercial cow feed. From the weekly body mass measurements, we estimated the percentage of cumulative mass loss from the mass of each individual at the onset of the experiment. This measurement of mass loss allowed us to compare individuals with different initial body mass. The percentage of cumulative body mass loss was used in all analyses.

To estimate forage intake, we recorded the time (±1 min) that each individual spent feeding at the trough and the amount of forage (±0.5 kg) eaten by the group at the end of each observation period. Time spent feeding included only the time that individuals were eating, with their head in the feeding trough. It was easy to estimate time spent feeding for each individual, because fawns were easy to identify and the surroundings of the trough were cleared of visual obstacles. Forage intake of each fawn was estimated from the product of the percentage of time spent feeding by an individual and the quantity of forage eaten by the group during the observation period. There was a strong positive correlation between total time spent feeding at the trough by all individuals and the amount of forage consumed, indicating that our estimate of forage intake was reliable (Taillon et al. 2006). All fawns were assumed to have similar bite sizes and feeding efficiency while eating at the troughs.

Experiments ended when snow melted and patches of food started to appear in the forest around the enclosure (mid-April in 2003 and late March in 2004), indicating that free-ranging fawns would have access to other food sources.

Ethical note

This study was part of a larger experiment testing the effects of naturally decreasing winter forage quality on the behaviour and life-history traits of captive white-tailed deer (Taillon et al. 2006). The treatment represented the winter diet expected for white-tailed deer on Anticosti Island in about 10–20 years (Potvin et al. 2003). We used the minimum number of fawns required for statistical analyses. We minimized disturbance to deer and only entered the enclosures once a day to feed the animals and clear snow from the scales. All observations were conducted in blinds. The levels of aggression of fawns and escalated fights were low and never led to any injuries or mortalities. Similarly to natural conditions, most fawns that weighed less than 26 kg in early winter died overwinter, but others had high survival (Taillon et al. 2006). In 2003, 4 of 13 fawns died (control diet: 2 of 7; poor diet: 2 of 6), and in 2004, 5 of 13 fawns died (control diet: 2 of 7; poor diet: 3 of 6). Fawns that died showed no obvious signs of distress before death. Necropsies revealed that deaths were probably due to starvation, based on very low marrow fat content of femurs, and that diet-quality treatment did not affect fawn mortality (Taillon et al. 2006). At the end of the experiment, all individuals were regrouped and fed with high-quality forage. After the fawns had gained weight, they were either released in the wild or translocated into large enclosures (20 and 40 ha) as part of a controlled-browsing experiment (see Tremblay et al. 2006). The Laval University Animal care and Use Committee approved all procedures (reference number 2001-275).

Statistical Analyses

Social hierarchies

Statistical analyses of social interactions were performed separately for the winters of 2003 and 2004. We used observations of agonistic encounters to establish the social hierarchy for all groups with Matman 1.0 for Windows (Noldus Information Technology 1998). We calculated the linearity of dominance hierarchies with the linearity index h' (de Vries 1995), which varies from 0 (absence of linearity) to 1 (complete linearity). This index is based on Landau's h, but it corrects for the number of unknown relationships.

To determine the statistical significance of linearity, we performed a resampling process using 10 000 randomizations (de Vries 1995). The outcome of dominance relationships was significantly linear, so we reorganized the dominance hierarchy using a two-step iterative procedure (1000 sequential trials) that ordered individuals first by minimizing the number of inconsistencies and then by the strength of inconsistencies (de Vries 1998; Côté 2000a). Inconsistencies are situations where individual j dominates i, but j is ranked below i in the hierarchy (de Vries 1998). The strength of an inconsistency is the absolute difference between the ranks of the two individuals that are involved in that inconsistency (de Vries 1998). Overall, the dominance matrices in our study were highly linear (Table 1), suggesting that social ranks would have

Table 1. Characteristics of the 2003 and 2004 winter dominance hierarchies of white-tailed deer fawns fed diets of different quality on Anticosti Island, Québec, Canada

Winter	Diet quality	Number of fawns	Number of interactions observed	Dyads observed (%)	h	h'	Directional consistency index (DC)	P
2003	Control	7	428	100	1	1	0.96	0.002
	Poor	6	415	93	0.80	0.83	0.95	0.08
2004	Control	7	214	90	0.80	0.84	0.90	0.05
	Poor	6	494	87	0.86	0.94	1	0.02

h = Landau's index of linearity (Landau 1951; de Vries 1995); h' = Landau's index of linearity corrected for the number of unknown relationships (de Vries 1995); P = linearity test using h' index, based on 10 000 randomizations (de Vries 1995); DC = from 0 (equal exchange) to 1 (complete unidirectionality) (van Hooff & Wensing 1987).

been similar if we had used other methods to determine ranks (Bayly et al. 2006). Although the hierarchy for the poor-quality diet group in 2003 was not significantly linear ($P = 0.08$; Table 1), we used the rank order after minimizing inconsistencies, because the hierarchy included only one inconsistency (see also Gendreau et al. 2005).

The number of ranked individuals varied between the experimental groups. To account for different numbers of individuals in the hierarchies, we transformed social ranks according to the formula: $1 - (\text{rank}/N_i)$ where N_i is the number of fawns alive during period i (Côté 2000a). Social rank therefore varied from 0 (subordinate) to 1 (dominant).

For each hierarchy, we calculated the directional consistency index (DC; van Hooff & Wensing 1987). DC is calculated across all dyads as the total number of interactions whose outcome is in the most frequent direction within each dyad (H) minus the number of interactions occurring in the less frequent direction (L) divided by the total number of interactions performed by all individuals ($DC = (H - L)/(H + L)$). The DC index ranges from 0 (equal exchange) to 1 (complete unidirectionality). Calculations were performed with Matman 1.0 for Windows (Noldus Information Technology 1998).

To determine whether individuals interacted more often with those that were closely ranked than with those that were more distant in the hierarchy, we compared the probability of initiating interactions against the three closest and the three most distant individuals in each hierarchy with paired Student's t tests.

To assess the potential effects of social rank and diet quality on aggressiveness, forage intake and body mass loss, we pooled the data from 2003 and 2004. Year was included as a random factor to control for stochastic between-year variation. Our sampling design included repeated observations of the same individuals. To avoid pseudoreplication, we used mixed models with random coefficients and analyses of covariance where each subject was treated as a covariable (Littell et al. 1996). In considering the subject as a random factor with repeated observations, we obtained linear models describing aggressiveness, forage intake and body mass loss variations for each individual.

Aggressiveness

To determine whether dominant individuals initiated more interactions (i.e. were more aggressive compared to

subordinates), we compared the number of interactions initiated by the three highest-ranking fawns and the three lowest-ranking fawns of each experimental hierarchy with a paired Student's t test.

Because our measure of aggressiveness was distributed between 0 and 1 and did not follow a normal distribution, we square-root transformed the aggressiveness data to meet assumptions of normality and homogeneity of variance. We used general linear mixed models (GLMM) to test the effects of diet quality, social rank, winter progression (Julian day) and all second-degree interactions on aggressiveness of fawns (mixed procedure, SAS Institute 8.0, Cary, North Carolina, U.S.A.). Year was considered as a random factor.

Forage intake

We also square-root transformed the forage intake data to meet the assumptions of normality and homogeneity of variance. We used general linear mixed models to test the effects of diet quality, social rank, winter progression (Julian day) and all second-degree interactions on forage intake of fawns (mixed procedure, SAS Institute 8.0).

Body mass loss

We used simple regression models to test the relation between body mass at the onset of winter and social rank of individuals (GLM procedure, SAS Institute 8.0).

Data on body mass loss were missing for a few individuals of different social ranks because they did not come often enough to the scale during winter to accurately estimate their decline in body mass. To analyse the effect of dominance status and diet quality on body mass loss, we grouped individuals into two categories of social rank: dominants, which included the three highest-ranking fawns in each diet group, and subordinates, which included the three or four lowest-ranking fawns in each diet group. We then used general linear mixed models to test the effects of diet quality, dominance status (dominants or subordinates group), winter progression (Julian days) and all second-degree interactions on percentage of cumulative body mass loss (mixed procedure, SAS Institute 8.0).

All data are presented as means $\pm$ SE. An α level of 0.05 was used to determine significance.
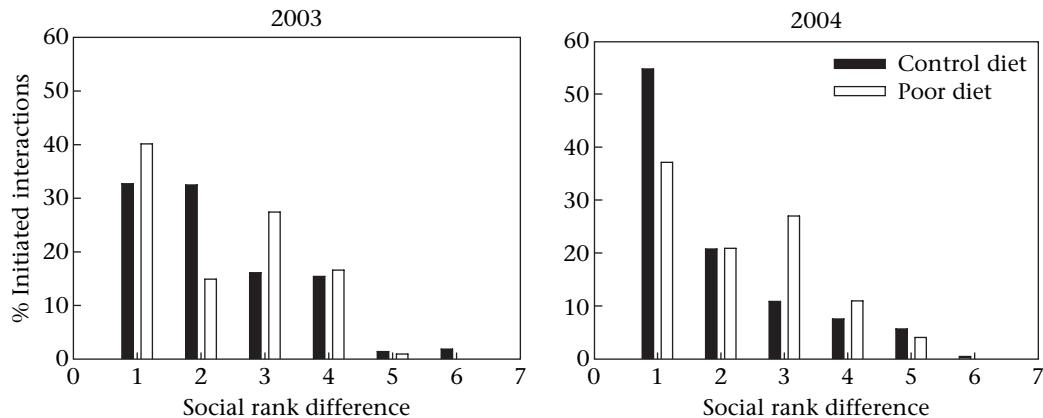
Figure 1. Percentage of agonistic interactions initiated in relation to the difference in social rank between individuals of each dyad for white-tailed deer fawns fed diets of different quality during the winters of 2003 and 2004 on Anticosti Island, Québec, Canada. Note that a social rank difference of 1 could be between two high-ranking individuals or between two low-ranking individuals.

RESULTS

Social Hierarchies

White-tailed deer fawns were consistently organized into linear hierarchies during both winters (Table 1). The hierarchies were stable, with only a few interactions directed towards higher-ranking fawns in 2003 (control diet: 2%; poor diet: 5%; $N = 843$) and in 2004 (control diet: 5%; poor diet: <1%; $N = 708$).

Fawns initiated more aggressive interactions towards the three fawns that were most closely ranked to them in the hierarchy than they did towards the three fawns that were most distantly ranked to them in the hierarchy during both winters (paired t test: 2003: control diet: $t_5 = -7.67$, $P = 0.002$; poor diet: $t_5 = -8.73$, $P = 0.0009$; 2004: control diet: $t_5 = -6.53$, $P = 0.003$; poor diet: $t_5 = -9.98$, $P = 0.0006$; Fig. 1).

Social rank was positively related to body mass at the onset of winter in each experimental group in winter 2003 (control diet: slope estimate $= 0.07 \pm 0.01$, GLM; $R^2 = 0.92$, $F_{1,5} = 49.50$, $P = 0.002$; poor diet: slope estimate $= 0.05 \pm 0.02$, GLM; $R^2 = 0.60$, $F_{1,5} = 6.04$, $P = 0.07$) and in 2004 (control diet: slope estimate $= 0.07 \pm 0.03$, GLM; $R^2 = 0.49$, $F_{1,6} = 4.86$, $P = 0.08$; poor diet: slope estimate $= 0.07 \pm 0.03$, GLM; $R^2 = 0.62$, $F_{1,5} = 6.40$, $P = 0.06$; Fig. 2). It was not possible to test for the influence of sex on social rank, because of the small sample sizes for each group. However, male fawns consistently occupied the first ranks in the hierarchies of both diet groups (Fig. 2).

Aggressiveness

Aggressiveness increased with social rank for both diets, so that dominant individuals were more aggressive than subordinate fawns, which were rarely aggressive (Table 2, Fig. 3). The three most dominant fawns in both diet groups initiated the majority of interactions in 2003 (control group: 85%; poor diet group: 99%; paired t test: $t_5 = -2.56$, $P = 0.03$) and in 2004 (control group: 76%;

poor diet group: 99%; $t_5 = -3.59$, $P = 0.008$). The interaction between social rank and winter progression was not significant (interaction day $\times$ rank, GLMM: $F_{1,22} = 0.01$, $P = 0.99$), indicating that dominant individuals remained more aggressive than subordinate individuals throughout the winter.

We detected a significant effect of the interaction between diet quality and winter progression on aggressiveness (Table 2). Aggressiveness of fawns fed the control diet remained constant or slightly increased during winter (all slopes positive except for two animals), whereas aggressiveness of fawns fed the poor-quality diet decreased throughout both winters (all slopes negative except for one animal). Despite different patterns of variation in aggressiveness according to diet quality during winter, diet quality as a single factor did not affect aggressiveness of fawns (Table 2), indicating that the average level of aggressiveness was similar for both diets.

Forage Intake

Subordinate fawns in both diet groups had higher forage intake than dominants (Table 2, Fig. 4). All fawns, however, irrespective of social rank, showed a similar decrease in forage intake during winter (interaction day $\times$ rank, GLMM; $F_{1,22} = 0.02$, $P = 0.89$; Table 2). As outlined in a companion study (Taillon et al. 2006), forage intake was also influenced by the interaction between diet and winter progression (Table 2): fawns fed the control diet decreased forage intake much more rapidly during the winter (slope estimate $= -0.11 \pm 0.01$, GLMM; $t_{22} = -9.15$, $P < 0.0001$) than fawns fed the poor-quality diet (slope estimate $= -0.04 \pm 0.01$, GLMM; $t_{22} = -2.80$, $P = 0.01$).

Cumulative Body Mass Loss

Body mass decreased for all fawns during the winter. Subordinate and dominant fawns lost body mass at a similar rate during winter and the percentage of
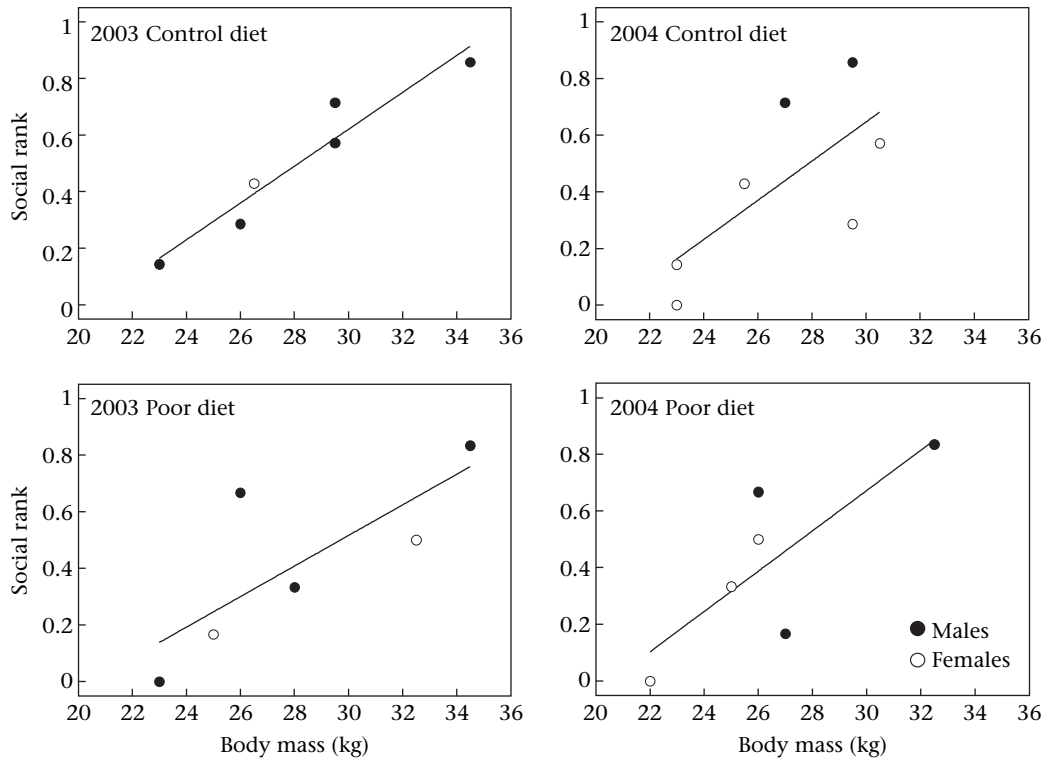
Figure 2. Relationship between body mass at the onset of winter and social rank of white-tailed deer fawns fed diets of different quality in 2003 and 2004 on Anticosti Island, Québec, Canada. Rank varies from 0 (subordinate) to 1 (dominant). Body mass at the onset of winter was missing for one female in the control group in 2003.

cumulative body mass loss did not differ with social rank or diet quality (Table 2; but see Taillon et al. 2006). The percentage of body mass loss at the end of the experiment was relatively high for both dominant (22.0 ± 1.0%) and subordinate (19.3 ± 1.4%) fawns.

Table 2. General linear mixed models of the effects of diet quality, social rank, winter progression (Julian day) and all second-degree interactions on aggressiveness, forage intake and cumulative body mass loss of white-tailed deer fawns fed diets of different quality during the winters of 2003 and 2004 on Anticosti Island, Québec, Canada

Factors	Effects	df	F	P
Aggressiveness	Day	22	2.05	0.17
	Diet	22	0.25	0.62
	Rank	22	33.58	<0.0001
	Day×diet	22	4.24	0.05
	Diet×rank	22	3.10	0.09
Forage intake	Day	22	70.19	<0.0001
	Diet	22	2.67	0.12
	Rank	22	11.49	0.003
	Day×diet	22	15.84	0.0006
Cumulative body mass loss	Day	17	987.33	<0.0001
	Diet	17	0.03	0.87
	Rank	17	0.01	0.94

Data from 2003 and 2004 were pooled, and year was included as a random factor. Nonsignificant ($P > 0.05$) statistical interactions are not shown and were not included in the final model. Aggressiveness is the number of interactions initiated by the focal individual divided by the number of opportunities of interactions.

DISCUSSION

Our study revealed that social rank and winter forage quality influenced the aggressiveness of white-tailed deer fawns. Using an experimental approach, we examined the effects of social dominance under restrictive winter foraging conditions on aggressiveness, forage intake and overwinter body mass loss. We hypothesized that an increase in the proportion of white spruce in the diet would have detrimental effects on several behavioural parameters and life-history traits of deer, but that those effects would be modulated by individual social rank (i.e. that the negative effects of a lower-quality diet would be stronger for subordinates than for dominants). Within diet-quality treatments, social rank was positively correlated with aggressiveness and negatively correlated with forage intake, but it did not influence body mass loss during winter. Between diet-quality treatments, diet quality, and its interaction with winter progression, affected aggressiveness and forage intake of fawns, but it did not affect body mass loss.

Adults in several ungulate species are organized into linear and stable dominance hierarchies (Thompson 1993; Côté 2000a; Veiberg et al. 2004). Although many studies have suggested that individuals learn their position within the dominance hierarchy early in their development (Thouless & Guinness 1986; Côté 2000a), there is little evidence to support this notion. We observed that white-tailed deer fawns were consistently organized into linear and stable hierarchies. During both winters, fawns initiated more aggressive interactions towards individuals
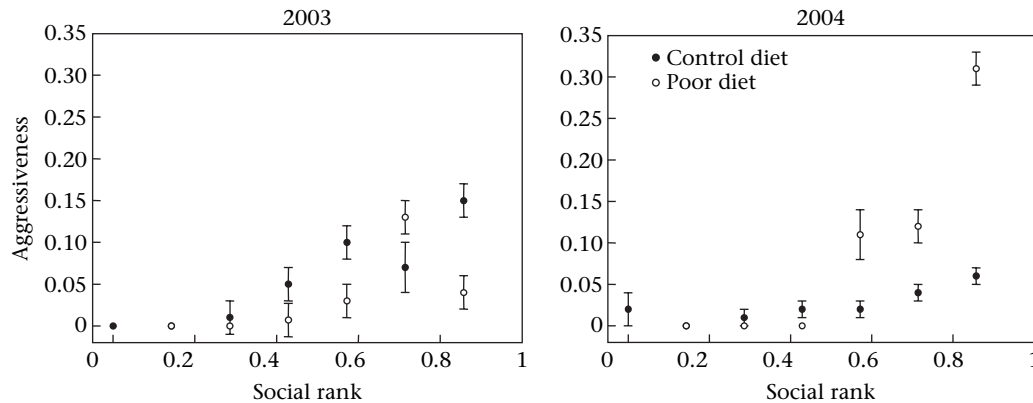
Figure 3. Aggressiveness (mean ± SE) of captive white-tailed deer fawns fed diets of different quality in relation to their social rank during the winters of 2003 and 2004 on Anticosti Island, Québec, Canada. Rank varies from 0 (subordinate) to 1 (dominant). Aggressiveness is the number of interactions initiated by the focal individual divided by the number of opportunities of interactions.

that were ranked most closely to them in the hierarchy than they did towards individuals that were ranked distantly to them in the hierarchy (Fig. 1). This is consistent with studies that have shown that individuals do not interact at random in social groups: they fight more frequently and intensely with individuals of close rank when the potential benefits of increasing rank are great, and they avoid fighting with individuals that they are unlikely to defeat and for which the costs of aggressive interactions may be high (Clutton-Brock et al. 1979, 1982; Barrette & Vandal 1986; Côté 2000a). The high directionality of aggressive interactions observed in our study (Table 1) may contribute to the long-term stability of the hierarchies (Thompson 1993; Côté 2000b) and suggests that potential advantages associated with a high rank established at an early age could endure into adulthood (Appleby 1982; Clutton-Brock et al. 1982).
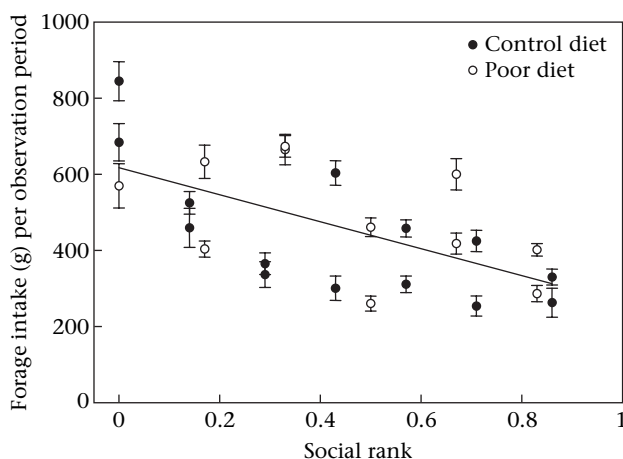
Figure 4. Forage intake of captive white-tailed deer fawns fed diets of different quality in relation to their social rank during the winters of 2003 and 2004 on Anticosti Island, Québec, Canada. Symbols represent mean ± SE forage intake per observation period (mean length: 5.44 ± 0.06 h) and the regression line is for pooled data from both diet groups.

Phenotypic traits such as body mass and body size can be used by animals to assess fighting ability of opponents (Reinhardt & Reinhardt 1975; Rutberg 1983) and are often positively correlated with dominance (Clutton-Brock et al. 1986; Kojola 1997; Holand et al. 2004; Veiberg et al. 2004). However, the influence of phenotypic traits is often mistaken with an effect of age, because older individuals are generally larger, more experienced and dominant over younger individuals (Alados & Escós 1992; Côté 2000a). Studying individuals of the same age class, we found that social rank was positively correlated with body mass at the onset of winter, with larger fawns achieving the highest social ranks. If high body mass increases the probability of achieving a high social rank, which could potentially increase individual fitness, then high body mass could be favoured by selection (Suttie 1982; Appleby 1982; Réale et al. 2000). Thus, the correlation between body mass and social rank at an early age may persist into adulthood and influence fitness (Suttie 1982; Kojola 1997; Gendreau et al. 2005).

We observed that dominant fawns initiated significantly more interactions and showed higher aggressiveness than subordinates (Fig. 3). Aggressiveness and social rank are also positively correlated in other ungulates (Appleby 1980; Eccles & Shackleton 1986; Thompson 1993; Araba & Crowell-Davis 1994; Barroso et al. 2000). In these studies, aggressiveness was associated with an increase in the probability of winning an encounter involving the access to a limited and valuable resource. However, social rank is not necessarily associated with aggressiveness (Clutton-Brock et al. 1976; Hall 1983; Fairbanks 1994; Côté 2000a): social dominance may create a stable social environment where the frequency of agonistic interactions and the energy costs and risk of injury associated with fighting are reduced (Maynard Smith 1974; Clutton-Brock et al. 1979; Hand 1986). The absence of a correlation between social rank and aggressiveness has been mostly observed in groups of animals where the costs of fighting are high (Clutton-Brock et al. 1979; Rutberg 1986) and the benefits associated with high social status are low (Hall 1983; Barroso et al. 2000). In our study, aggressiveness was positively related to social rank, suggesting that the

costs of fighting may be low or that the benefits conferred by the contested resource may be high. We did not observe escalated interactions or great differences in the intensity of aggressive behaviours used throughout the winter, suggesting low costs of fighting for fawns. However, the true energetic costs of aggressiveness remain to be measured.

Increased aggressiveness or high dominance status may favour access to scarce resources that provide benefits. In many large herbivores, dominant individuals often monopolize foraging sites that maximize energy intake (Appleby 1980; Rutberg 1986; Alados & Escós 1992; Barroso et al. 2000) and show longer foraging times than subordinates (Lovari & Rosto 1985; Barrette & Vandal 1986). In our study, however, we observed the opposite effect: subordinate fawns showed higher forage intake than dominant fawns during both winters, even when each fawn had the same access to the trough (Table 2, Fig. 4). Subordinate fawns may have suffered the costs of receiving, avoiding and escaping aggressive interactions from dominant fawns. As suggested by several studies (Thouless & Guinness 1986; Côté 2000a; Forkman & Haskell 2004), dominance relationships could be based on the outcome of the first aggressive encounters between two individuals, and dominant animals may then frequently attack subordinates to condition them to lose in future encounters. We suggest that the energetic costs associated with receiving and avoiding aggressive interactions may have caused subordinates to increase their forage intake compared to dominants, so that they could present a similar body mass loss as dominant fawns during winter.

Dominance, however, could be an advantage to individuals when resources are clumped rather than diffuse in the environment. We observed that dominant individuals were always the first ones on the weighing scale to access the bait. Under natural winter conditions, where forage distribution is patchy and energetic constraints associated with finding forage and cover are high (Beier & McCullough 1990; Parker et al. 1999), a high dominance status could help to ensure access to forage and reduce overwinter body mass loss. On Anticosti Island, a large proportion of winter forage comes from fallen trees, so individuals of high social rank probably have an advantage gaining access to and monopolizing this concentrated forage resource.

During the annual life cycle, aggressiveness can be modulated both by the value of the contested resources and by changes in body condition (Appleby 1980; Rutberg 1986; Grenier et al. 1999). During winter, as the quality and availability of forage resources decrease, body condition and risk of starvation can change markedly (Moen 1978; Verme & Ullrey 1972). We observed that diet quality during winter influenced aggressiveness of fawns: fawns fed the control diet maintained their aggressiveness level throughout the winter, whereas fawns fed the poor-quality diet decreased it. Diet quality also influenced forage intake: fawns fed the poor-quality diet decreased their forage intake at a much lower rate during winter than did the controls (Table 2; Taillon et al. 2006). We suggest that the decrease in aggressiveness and the higher forage intake observed for fawns fed the poor-quality diet, regardless of their social rank, may represent a behavioural strategy to minimize body mass loss over winter and, possibly, to compensate for their similar mass loss as control animals. Body condition may determine the energy allocated to aggressive behaviours throughout the winter (Appleby 1980; Barrette & Vandal 1986; Grenier et al. 1999), so fawns on the poor-quality diet could have been forced to decrease expenditures associated with aggressive behaviours.

Using an experimental design controlling for winter diet quality, we asked questions that could not be answered under natural winter conditions. In the future, similar experiments could simulate the patchy distribution of winter forage to examine the importance of dominance status in relation to access to clumped versus dispersed forage, and forage of different quality. Such experiments could also be useful to better understand the relationship between dominance status and aggressiveness, and to clarify the benefits and costs associated with high dominance and aggressiveness. White-tailed deer responded to a reduction in winter forage quality by modifying their aggressiveness, indicating that ungulates may show plasticity not only in their foraging behaviour in response to decreased resources but also in their social behaviour.

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