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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.

Keywords: aggressiveness; agonistic behaviour; body mass loss; dominance status; forage intake; *Odocoileus virginianus*; resource competition; social behaviour; white-tailed deer; winter forage quality

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).