



The role of previous social encounters and body mass in determining social rank: an experiment with white-tailed deer

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The social organization of many vertebrates is based on dominance behaviours occurring between pairs of individuals. Initial encounters between any two individuals can be crucial in determining the dominance relationship that will prevail between them throughout their lifetime. Achieving a high dominance status can be critical when competition for limited resources such as foraging sites is intense. The mechanisms that prevail for the establishment and stability of dominance relationships between individuals are, however, poorly understood. Our study aims to identify factors influencing the establishment of dominance relationships between young individuals, using white-tailed deer, *Odocoileus virginianus*, fawns as a model species, and to evaluate the possibility of long-term individual recognition after temporal separation. We used an experimental approach to test the alternative hypotheses that dominance relationships after temporal separation are explained by (1) the outcome of the previous encounters between opponents or (2) the body mass difference between individuals independently of the outcome of initial encounters. Social rank was established during the first encounters between individuals based on differences in body mass and was maintained afterwards even when the differences in mass between individuals were reversed. Our results suggest that individual long-term recognition may influence the outcome and the stability of dominance relationships after temporal separation of individuals. Dyadic dominance relationships seem to be established early in life and may then endure into adulthood.

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In social species, achieving a high social rank can be critical when competition for limited resources such as feeding sites, bedding sites, or sexual partners is intense (Appleby 1980; Barrette & Vandal 1986). One major advantage for dominant individuals is priority access to limited resources, such as food, that can increase their body condition and may then lead to a higher feeding efficiency (Lovari & Rosto 1985; Rutberg 1986; Thouless 1990), increased access to mates (Clutton-Brock et al. 1979), higher reproductive success (Dunbar & Dunbar 1977; Côté & Festa-Bianchet 2001) or lower risk of predation (van Noordwijk & van Schaik 1987) compared to subordinates. Dominance may be particularly advantageous at high population density and during food shortages (Clutton-Brock et al. 1986; Albon et al. 1992).

The social organization of many vertebrates is based on dominance behaviours (Drews 1993). Dominance refers to the result of agonistic interactions occurring between pairs

of individuals or dyads (Drews 1993). In a linear dominance hierarchy, each individual occupies a specific social rank based on the outcome of all dyadic dominance relationships. In many ungulates, social rank is positively correlated with individual traits such as age, body mass and antler size (Appleby 1982; Suttie 1982; Barrette & Vandal 1986; Côté 2000a; Holand et al. 2004), presumably because an individual's decision to engage in aggressive interactions depends largely on the opponent's phenotypic traits (Reinhardt & Reinhardt 1975; Rutberg 1983). Within a specific age class, males are usually dominant over females (Townsend & Bailey 1981; Hall 1983; Byers 1997). Dominance relationships often depend on body mass (Hirotani 1990; Locati & Lovari 1991; Veiberg et al. 2004), but not consistently, even within the same species (Bouissou 1972; Rutberg 1983; Eccles & Shackleton 1986). Several studies have shown that the influence of body size or body mass is confounded with age (Alados & Escós 1992; Côté 2000a), because older individuals, which are more experienced and usually bigger, are often dominant over younger ones. Studies on dominance should consider this age-dependent effect either by accounting for the

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effects of age on rank before assessing the relationship between rank and body size (Côté 2000a) or by focusing on a specific age class of the population, such as young of the year (Robinson 1962; Townsend & Bailey 1981; Suttie 1982).

Few studies have focused on social interactions during the first year of life in mammals (Robinson 1962; Townsend & Bailey 1981; Byers 1997). In social species, however, individuals start to interact at a young age and it has been hypothesized that individuals learn their position within the dominance hierarchy early in their development (Thouless & Guinness 1986; Côté 2000a). In this context, the first encounters between any two individuals can be crucial in determining the dominance relationship that will prevail between them throughout their lifetime (Barrette & Vandal 1986; Holand et al. 2004). Once dyadic dominance relationships are defined, a stable social hierarchy can be maintained in a group with only rare challenges (Rutberg 1983; Alados & Escós 1992; Thompson 1993; Côté 2000a). Studies have shown that dominance relationships may be maintained largely by threat signals seldom involving physical contact (Bouissou 1972; Eccles & Shackleton 1986; Côté 2000a). The occurrence of a dominance hierarchy creates a stable social environment and hence reduces the energetic costs and the risk of injury associated with aggressive behaviours (Clutton-Brock et al. 1986; Hand 1986; Jackson 1988).

The composition of groups in social species, however, is often unstable, and individuals can be separated during relatively long periods (e.g. seasons) and rejoin afterwards. When individuals meet again after a period of separation, their dominance relationships may (1) depend on phenotypic traits such as body mass, so that larger individuals would be dominant over smaller individuals, regardless of the outcome of the initial encounters between them or (2) be identical to those that were established during initial encounters, and hence may be based on the long-term recognition between individuals, regardless of any reversals in body mass that may have occurred during the separation.

We tested the effects of sex and body mass on the establishment of dominance relationships in white-tailed deer, *Odocoileus virginianus*, and evaluated the possibility of long-term individual recognition after temporal separation. We used an experimental approach to test the alternative hypotheses that after temporal separation, dominance relationships among young white-tailed deer would be explained by (1) the outcome of the previous encounters between opponents or (2) the difference in body mass between the two individuals independently of the outcome of initial encounters.

METHODS

Study Area

The experiment took place on Anticosti Island (7943 km²), Gulf of St Lawrence, Québec, Canada. The sub-boreal maritime climate is characterized by cool summers and long winters (Huot 1982). Vegetation is classified

as subArctic, and the main tree species found on the island are balsam fir, *Abies balsamea*, white spruce, *Picea glauca*, and black spruce, *Picea mariana* (Potvin et al. 2003). No indigenous large herbivores were present on the island before the introduction of approximately 220 white-tailed deer in the late 1800s (Côté 2005). The population erupted in the absence of natural predators and local densities now reach more than 20 deer/km² (Potvin & Breton 2005). The high deer density on the island has had major impacts on the native flora, mainly on herb and shrub layers, and there is very little winter browse available (Potvin et al. 2003).

Captures

We captured 32 white-tailed deer fawns during 24 November–11 December 2002 ($N = 19$) and 28 November–25 December 2003 ($N = 13$) using physical and chemical immobilization (Taillon et al., in press). Fawns were captured at multiple baiting sites distributed over an area of approximately 120 km², so it is unlikely that they had interacted before the experiment. In the rare cases where individuals might have been in contact before the experiment (i.e. capture sites within about 2 km), they were put in different groups during winter. Sex of fawns was determined and they were weighed to the nearest 0.5 kg with a spring scale or an electronic platform scale. We measured hind foot length to the nearest 0.5 mm. All fawns were individually marked with plastic eartags and released into an outdoor enclosure. The Laval University Animal Care and Use Committee approved all procedures.

Experimental Design and Pre-experimental Period

We established an 80 × 150-m enclosure surrounded by a 4-m-high game fence in a natural and mature white spruce stand where trees did not have branches lower than 3 m and the shrub layer was absent, thereby excluding any uncontrolled food input into the enclosure except litterfall. The enclosure was further subdivided into three sections of 80 × 50 m each with 30–40% of the initial forest maintained as cover. Three basic wooden structures were built in each section to simulate wind-protected areas in the natural forest. This experimental set-up was part of a companion study addressing the effects of winter nutrition on deer body condition and social behaviour (Taillon et al., in press).

During the pre-experimental periods (19 December 2002–11 January 2003 and 27 December 2003–8 January 2004), fawns were grouped together and had free access to the first two sections of the enclosure. They were fed with a diet similar to that of free-ranging fawns during winter on Anticosti (i.e. 70% balsam fir, 20% white spruce and 10% arboreal lichens; Huot 1982; Lefort 2002). Fresh branches were collected every 2–3 days and shredded separately in a wood chipper (Yard Machines-5 HP chipper) to create a uniform mixture that prevented fawns from selecting one of the diet components. Using microhistological analyses of faeces, we

verified that fawns ate the proportion of spruce and fir given to them (Taillon et al., *in press*). Food was placed into a single feeding trough (2.5 m × 30 cm × 30 cm). 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). We used spotting scopes (15–25×) and binoculars (8 × 42) to conduct behavioural observations from elevated blinds situated 30–40 m from the feeding troughs. We used ad libitum sampling (Altmann 1974) to record aggressive interactions during 60 h of observation each year. 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.

Experimental Period

As part of a companion study (Taillon et al., *in press*), the fawns were randomly divided into groups of similar size and sex composition and fed diets of different qualities during winter. The experimental diets were composed of different proportions of white spruce and a mixture of balsam fir and arboreal lichens. The control diet (20% spruce) represented the actual winter diet composition of free-ranging deer on Anticosti (Lefort 2002). The poor diet included 40% spruce. We predicted a positive relationship between body mass loss overwinter and the proportion of white spruce in the diet that would create opportunities to assess the effects of body mass loss on social rank at the end of the winter (Taillon et al., *in press*).

Postexperimental Period

At the beginning of April, we regrouped the surviving fawns together. The postexperimental period lasted from 21 April to 1 May in 2003 and from 27 March to 5 April in 2004 because snow melted earlier in 2004. Twelve fawns survived (58%) in 2003 and eight (62%) in 2004. These survival rates are comparable to what is found naturally, as mortality can reach 40% during winter on Anticosti Island even in the absence of predation (Potvin et al. 1997). Necropsies revealed that fawns who did not survive likely died of starvation, as suggested by their very low femur marrow fat content (Taillon et al., *in press*). Mortality rate, however, did not differ according to diet quality (Taillon et al., *in press*). During the postexperimental period, individuals were fed the control diet. We noted ad libitum agonistic interactions between pairs of individuals during 60 h of observations each year. We measured the body mass of fawns (± 0.5 kg) using a platform scale baited with cow feed. We used body mass in all analyses. However, we also performed analyses using a body condition index estimated either by dividing body mass (kg) by hind foot length (cm) to take into account structural

size (Clutton-Brock & Pemberton 2004) or by using the residuals of body mass regressed on hind foot length (Schulte-Hostedde et al. 2005). We obtained the same conclusions with these three measurements and, for simplicity, we only present results for body mass. At the end of the study, all surviving fawns were translocated to large summer enclosures as part of a controlled browsing experiment (Côté et al., *in press*).

Statistical Analyses

The analyses were performed separately for the winters of 2003 and 2004. We used ad libitum 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 the pre-experimental and the postexperimental 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 unlike h , h' corrects for the number of unknown relationships.

To determine the statistical significance of linearity, we performed a sampling process using 10 000 randomizations (de Vries 1995). If significantly linear, the dominance hierarchy was reorganized by a two-step iterative procedure (1000 sequential trials) that first ordered individuals by minimizing the number of inconsistencies and then the strength of these inconsistencies. Inconsistencies are situations where individual j dominates i , but j is ranked below i in the hierarchy (de Vries 1998). The strength of inconsistencies is the absolute difference between the ranks of two individuals that are involved in an inconsistency (de Vries 1998).

The number of individuals ranked varied between the pre- and the postexperimental periods. 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 ranks therefore varied from 0 (subordinate) to 1 (dominant).

We used linear models to test the effects of sex and body mass on pre-experimental social ranks (proc GLM, SAS Institute 8.0, Cary, North Carolina, U.S.A.). To assess whether pre-experimental social rank or body mass was the most influential factor in determining postexperimental social rank, we entered them in alternation in simple regression models. We also examined the relation between individual overwinter loss of body mass (%) and pre-experimental social rank to determine whether individuals that lost more mass overwinter were those that had a low social rank in early winter (proc GLM, SAS Institute 8.0).

We analysed each dyad to determine whether changes in social rank between the pre- and postexperimental periods were associated with a reversal in body mass rank. We identified each dyad where individuals changed positions in the social hierarchy and/or showed reversals in body mass from the pre- to the postexperimental period and analysed the data in a two-way contingency table (proc FREQ, SAS Institute 8.0). In 2004, only two dyads

experienced a reversal of body mass or social rank, precluding statistical analysis for that year. All statistical analyses were performed with SAS (SAS Institute 8.0) and all data are presented as means \pm SE.

RESULTS

Pre-experimental Social Hierarchy

White-tailed deer fawns were highly social and therefore most dyads were observed interacting (Table 1). Fawns were organized in a significantly linear social hierarchy during the pre-experimental period in both years (Table 1). The hierarchies were stable, with only 9% (2003) and 3% (2004) of all interactions directed towards higher-ranking fawns.

In both years, social rank did not differ significantly between sexes during the pre-experimental period (2003: GLM: $F_{1,18} = 1.55$, $P = 0.23$; 2004: $F_{1,12} = 3.81$, $P = 0.08$). In 2003, however, male fawns occupied the first six ranks (average rank: males: 0.53 ± 0.08 ; females: 0.35 ± 0.12) in the hierarchy, and in 2004, they occupied the first two ranks (males: 0.65 ± 0.12 ; females: 0.35 ± 0.10). Pre-experimental social rank was positively associated with body mass in both years (2003: slope estimate = 0.06 ± 0.01 , GLM: $R^2 = 0.61$, $F_{1,16} = 22.34$, $P = 0.0003$; 2004: slope estimate = 0.07 ± 0.02 , $R^2 = 0.48$, $F_{1,13} = 10.03$, $P = 0.009$; Fig. 1a, b).

Postexperimental Social Hierarchy

At the end of the winter, regrouped fawns were also organized in a significantly linear social hierarchy in both years (Table 1). The postexperimental hierarchies were stable, with only 1% of all interactions directed towards higher-ranking fawns in both years. To verify that previous experience in the enclosure did not affect social rank, we compared ranks of fawns who were moved to different enclosures with ranks of fawns who were not moved, and we found no difference (two-tailed t test: 2003: $t_9 = 0.59$, $P = 0.57$; 2004: $t_6 = -0.14$, $P = 0.89$).

In 2003, there were 55 dyads in the postexperimental period: 10 dyads showed a reversal in body mass and nine dyads showed a reversal in social rank, compared to the pre-experimental period. Only one reversal in social rank was associated with a corresponding change in body mass. From the pre- to the postexperimental period, therefore,

reversals in social rank were not related to changes in body mass (contingency table: $\chi^2 = 0.36$, $N = 55$, $P = 0.55$). In 2004, there were 28 dyads in the postexperimental period: no dyad experienced a reversal in body mass and one dyad experienced a reversal in social rank, compared to the pre-experimental period. The only reversal in social rank observed was not associated with a corresponding change in body mass.

In 2003, postexperimental social rank was positively associated with both body mass at the end of the winter (slope estimate = 0.10 ± 0.02 , GLM: $R^2 = 0.70$, $F_{1,10} = 18.61$, $P = 0.003$; Fig. 1c) and pre-experimental social rank (slope estimate = 0.83 ± 0.18 , GLM: $R^2 = 0.70$, $F_{1,11} = 20.68$, $P = 0.001$; Fig. 2a). In 2004, postexperimental social rank was strongly and positively associated with pre-experimental social rank (slope estimate = 0.98 ± 0.09 , GLM: $R^2 = 0.95$, $F_{1,7} = 121.52$, $P < 0.0001$; Fig. 2b) and, unlike in 2003, it was not correlated with body mass at the end of the winter (slope estimate = 0.05 ± 0.05 , GLM: $R^2 = 0.16$, $F_{1,7} = 1.15$, $P = 0.33$; Fig. 1d).

Finally, overwinter loss of body mass was not related to pre-experimental social rank, suggesting that high- and low-ranking individuals lost mass at a similar rate during the winter (2003: GLM: $F_{1,8} = 0.31$, $P = 0.59$; 2004: $F_{1,7} = 0.00$, $P = 0.95$).

DISCUSSION

Our results provide evidence that social rank is established during the initial encounters between individuals based on differences in body mass and is thereafter maintained over several months even when the differences in mass between individuals change. In both winters of our study, the pre-experimental social ranks of white-tailed deer fawns were positively related to body mass. After 3 months of separation, however, social rank was related to body mass only in 2003 and not in 2004. Pre- and postexperimental social ranks were highly correlated in both years, suggesting long-term individual recognition and maintenance of dyadic dominance relationships established early in life despite changes in mass.

During both the pre- and postexperimental periods, white-tailed deer fawns were organized into stable and highly linear social hierarchies (Table 1), as observed in several ungulate species (Rutberg 1983; Thompson 1993; Côté 2000a; Holand et al. 2004; Veiberg et al. 2004). Interactions between individuals were frequent and the

Table 1. Characteristics of the 2003 and 2004 pre- and postexperimental dominance hierarchies of white-tailed deer fawns on Anticosti Island, Québec, Canada

| Winter | Period | Number of fawns | Number of aggressive interactions observed | % Dyads observed | h | h' | P |
|--------|------------------|-----------------|--|------------------|------|------|---------|
| 2003 | Pre-experimental | 19 | 668 | 74 | 0.60 | 0.63 | <0.0001 |
| | Postexperimental | 11 | 83 | 54 | 0.45 | 0.56 | 0.02 |
| 2004 | Pre-experimental | 13 | 272 | 76 | 0.72 | 0.77 | 0.0002 |
| | Postexperimental | 8 | 293 | 86 | 0.88 | 0.93 | 0.0002 |

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).

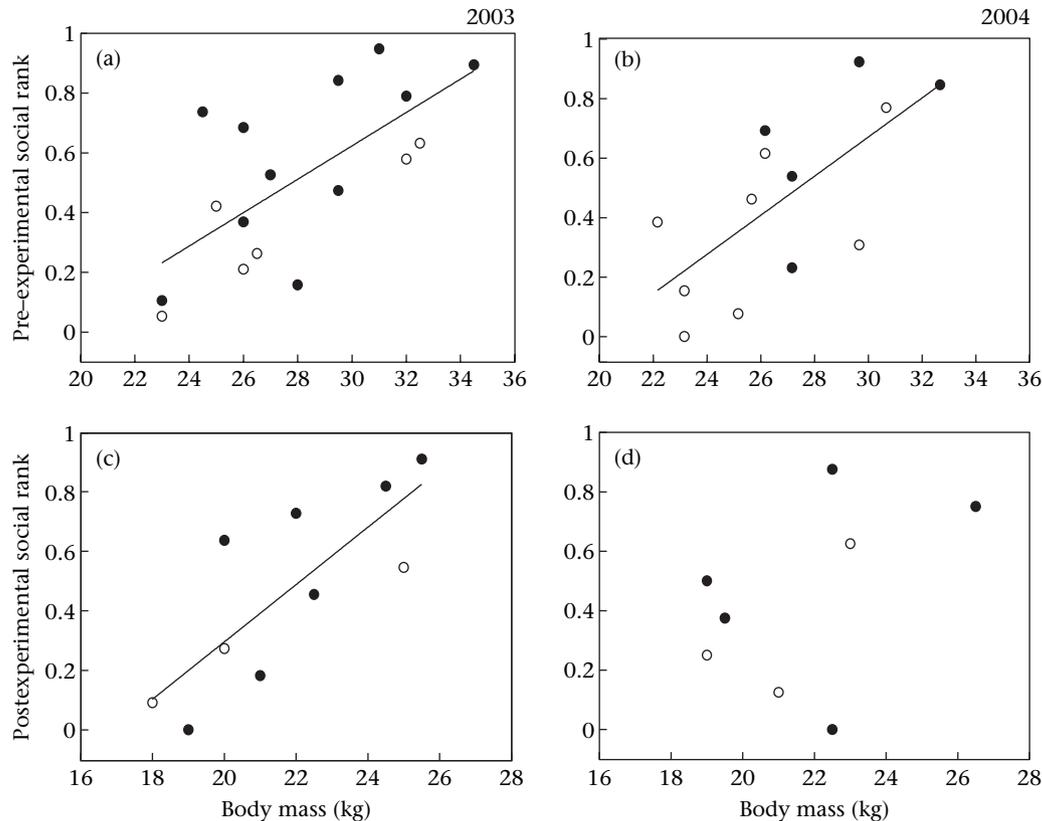


Figure 1. Relationships between body mass and pre-experimental (a, b) and postexperimental (c, d) social ranks of white-tailed deer fawns, in 2003 and 2004, on Anticosti Island, Québec, Canada. ●: males; ○: females. Regression line for significant effects is for both sexes pooled.

outcomes of interactions were clear and rapidly resolved. It has been reported that individuals learn their positions within the dominance hierarchy early in their development (Thouless & Guinness 1986; Datta 1988; Côté 2000a). The first encounters between any two individuals can be crucial in determining the dominance relationship that will prevail between them throughout their lifetime (Barrette & Vandal 1986; Holand et al. 2004). The existence of a dominance hierarchy may also create a stable social environment and hence may reduce the energetic costs and the risk of injury associated with aggressive behaviours, particularly in species possessing dangerous weapons such as the antlers of deer or the horns of bovids (Clutton-Brock et al. 1986; Hand 1986).

Unlike other studies on mature ungulates (Townsend & Bailey 1981; Hall 1983), sex did not significantly affect the establishment of pre-experimental social rank of fawns in either year. Male fawns, however, always occupied the first ranks within hierarchies. An effect of sex on social rank could be related to differences in body mass (Holand et al. 2004; Veiberg et al. 2004). Robinson (1962), for example, noted that male fawns are usually larger than females and achieve higher social ranks. We suggest that the absence of sexual dimorphism in fawns on Anticosti (A. Simard & S. D. Côté, unpublished data) and the small size of our experimental groups precluded us from detecting an effect of sex on social rank.

We found that pre-experimental social rank was strongly and positively associated with body mass in

both years (Fig. 1a, b). Several studies on ungulates have reported that dominance relationships were primarily determined by phenotypic traits such as body mass and body size (Reinhardt & Reinhardt 1975; Clutton-Brock et al. 1986; Kojola 1997; Veiberg et al. 2004) or antler length (Barrette & Vandal 1986; Holand et al. 2004). Body mass can easily be evaluated by animals and is considered a reliable measure of fighting ability (Reinhardt & Reinhardt 1975; Rutberg 1983). However, in our study, body mass explained 50–60% of the variability in pre-experimental social rank in both years, suggesting that factors other than body mass can be of importance in determining the outcome of contests. For example, birthdate might affect the probability of winning an encounter among fawns (Byers 1997). In addition, individual differences in temperament are not necessarily related to body mass, but may affect how animals behave in a variety of social contexts and, therefore, influence the outcome of dominance relationships (Réale et al. 2000).

Unlike the pre-experimental period, body mass was not the most important factor determining postexperimental social rank in white-tailed deer fawns. We found that dominance relationships were maintained from the pre- to the postexperimental period, because postexperimental social rank was highly correlated to pre-experimental social rank in both years (Fig. 2). In spite of reversals in body mass between individuals of some dyads during the winter, dominance relationships remained stable. Individuals that became smaller than their opponent in

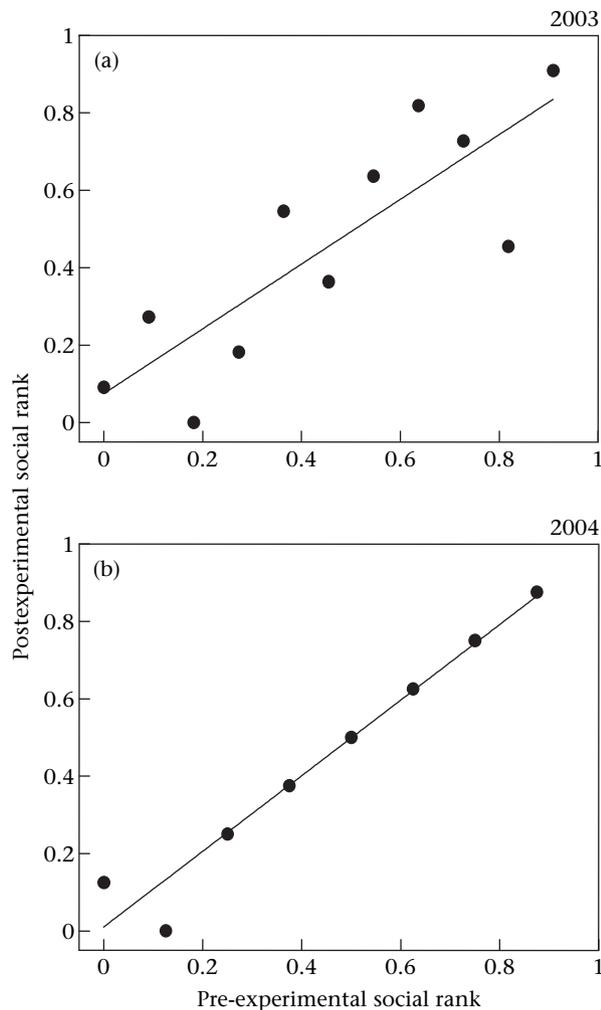


Figure 2. Relationships between pre- and postexperimental social rank of white-tailed deer fawns, in 2003 (a) and 2004 (b), on Anticosti Island, Québec, Canada.

dyads of the postexperimental period remained dominant if they were also dominant during the pre-experimental period. Berdoy et al. (1995) found that the determination of social ranks during the first encounters in wild rats, *Rattus norvegicus*, was highly correlated with body mass. Over time, however, individuals remained dominant over subordinates even if initial body mass asymmetries disappeared. These results support our findings that the initial determination of dominance relationships between white-tailed deer fawns may persist in time, even though the body mass difference between dyad members changes. The stability of the social hierarchy from early to late winter suggests that re-establishing social rank after separation may involve some costs (e.g. through fighting) associated with achieving a high social rank; otherwise, individuals would challenge each other.

Several studies have observed highly stable dominance hierarchies over time (Hausfater et al. 1982; Rutberg 1983; Côté 2000a), but were also investigating relatively stable groups. Very few attempts have been made to study the variations in dominance relationships between individuals that have been separated during seasonal periods.

Fairbanks (1994; female pronghorn: *Antilocapra americana*) and Thompson (1993; female sable antelope: *Hippotragus niger*) noted that temporary absence of established herd members did not affect their social rank in the herd. The dominance relationships between individuals that were separated remained unchanged when they reunited following prolonged separation.

The stability of social rank of white-tailed deer fawns over time suggests that individual long-term recognition is based on traits such as physical attributes or olfactory cues. Holand et al. (2004) suggested that the determination of dominance relationships between individuals in reindeer, *Rangifer tarandus*, can involve visual assessment of physical attributes. These physical attributes, however, remain to be identified. Miller et al. (1998) studied urinary volatile compounds from male and female mature white-tailed deer and found that the presence and concentration of different urinary compounds depended on season, reproductive status and social rank. Urine samples collected from dominant and subordinate deer showed differences in the presence and concentration of chemical compounds such as alcohols, ketones and alkanes. They suggested that these differences in urine composition may produce odours that are correlated with social rank. Given the importance of urine in olfactory communication in white-tailed deer (Gassett et al. 1997), individual differences in urinary volatile compounds and in secretions from various glands such as the tarsal and interdigital glands (Gassett et al. 1996; Osborn et al. 2000) may be involved in individual recognition and identification of social status.

We have shown that body mass influences the social rank of fawns in early winter. This could have significant consequences because dominant and large fawns may have better access to forage at the beginning of the winter, and may therefore experience a smaller overwinter body mass loss than subordinate fawns. In our study, however, overwinter loss of body mass was not related to pre-experimental social rank, indicating that high- and low-ranking individuals lost similar body mass during the winter and that being dominant did not seem to confer nutritional advantages during winter. The main determinant of winter survival, however, was body mass at the onset of winter (Taillon et al., in press). In our experimental design, forage was available ad libitum and easily accessible to all fawns. As our set-up favoured agonistic interactions without limiting individual access to food, there might have been no priority access advantage for dominants. In 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), dominance status may be of greater importance for priority access to food.

Conclusion

Body mass was the main factor determining social rank of white-tailed deer fawns in early winter, but not in late winter. Dominance relationships were maintained throughout the winter, despite reversals in body mass

that occurred during the separation. Our experiment therefore provides support for the hypothesis that, after temporal separation, dominance relationships are explained by the outcome of previous encounters between opponents and not by postseparation body mass. Our results also suggest that individual long-term recognition may influence the outcome and the stability of dominance relationships after temporal separation of individuals. Dyadic dominance relationships seem to be established early in life and maintained after temporal separation, suggesting that an individual's social rank as a juvenile persists into adulthood.

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