Determinants and life-history consequences of social dominance in bighorn ewes

MAGALI FAVRE*, JULIEN G. A. MARTIN*† & MARCO FESTA-BIANCHET*†

*Département de Biologie, Université de Sherbrooke
†Centre d'Études Nordiques, Université Laval, Québec City

Studies of social rank in female ungulates consistently suggest that dominance increases with age, perhaps because dyadic relationships are established early in life, when the older female is always larger than the younger one. This relationship then remains unchanged, even if for fully grown adults size and age are not correlated, suggesting that typically female ungulates normally gain little from being dominant. In contrast, social interactions among 64 marked known-age bighorn sheep ewes (*Ovis canadensis*) over 3 summers at Ram Mountain, Alberta, Canada, suggest that the effect of age on social rank weakened substantially for ewes older than 6 years. Mass was strongly related to rank for ewes age 7 years and older, whereas horn size had no effect on dominance. Once they reach asymptotic mass, bighorn ewes appear to challenge older but lighter females to whom they were formerly subordinate. Although these results suggest that bighorn ewes may benefit from high social rank, we found no effect of rank on reproductive success, lamb sex ratio or lamb birth date.

Dominance is an attribute of the pattern of repeated agonistic interactions between two individuals, characterized by a predictable outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation (Drews 1993). Social dominance has been studied in many mammals because of its importance in reproductive success, especially for males (Hass & Jenni 1991; Haley et al. 1994; Pelletier & Festa-Bianchet 2006). Among female ungulates, body mass (Hirotani 1990; Veiberg et al. 2004; Vervaecke et al. 2005), age (Rutberg, 1986; Festa-Bianchet 1991; Côté 2000; Archie et al. 2006) and a combination of age and mass (Kojola 1989; Locati & Lovari 1991; Holand et al. 2004a) have been reported as the main attributes determining rank. The high covariations of these attributes, however, hinder both the statistical analyses and the interpretations of results. Thouless & Guiness (1986) suggested that in red deer hinds, *Cervus elaphus*, the dominance relationship within each dyad is established early in life, when the older

female is heavier than the younger one and is therefore dominant. That relationship is then maintained later in life, even if by then the younger female may be larger than the older one. Inertia in the female dominance relationship suggests that there may be few advantages in being dominant, so subordinates have little to gain by attempting to improve their social rank (Taillon & Côté 2006). Strongly age-related hierarchies are frequently reported for female ungulates (red deer, Thouless & Guiness 1986; mountain goats, *Oreamnos americanus*, Côté 2000, Fournier & Festa-Bianchet 1995; white-tailed deer, *Odocoileus virginianus*, Townsend & Bailey 1981; American bison, *Bison bison*, Rutberg 1986; bighorn sheep, *Ovis canadensis*, Festa-Bianchet 1991). It may be difficult for dominant female ungulates to monopolize food, particularly for grazers, because grass is generally uniformly and widely distributed. However, if vegetation is patchy, dominance could affect access to forage. For northern ungulates, forage may be very patchy and difficult to access in winter, when craters must be dug in snow (Barrette & Vandal 1986). Holand et al. (2004a) reported a strong effect of both age and body mass on social rank in reindeer, *Rangifer tarandus*, females. In winter, dominant females gained mass and subordinates lost mass (Holand et al. 2004b).

Correspondence: M. Festa-Bianchet, Université de Sherbrooke, 2500, Boulevard de l'université, Sherbrooke, Québec J1K 2R1, Canada (email: marco.festa-bianchet@usherbrooke.ca).

The reproductive success of female ungulates is directly linked to their ability to obtain resources (Clutton-Brock et al. 1981). Maternal dominance in gregarious ungulates has rarely been reported to affect lifetime reproductive success (Clutton-Brock et al. 1986; Holand et al 2004b), but few studies have obtained the data required to test this relationship. Previous studies on bighorn ewes suggested that dominance was unrelated to reproductive success (Eccles & Shackleton 1986; Festa-Bianchet 1991; Hass 1991).

Female dominance in ungulates may also be associated with adaptive manipulations of offspring sex ratio. Trivers & Willard (1973) proposed a model of adaptive sex ratio bias based on maternal condition and on the differing returns of additional maternal care according to offspring sex. In polygynous mammals with strong sexual dimorphism, reproductive success is expected to be more variable for males than for females. Consequently, mothers in good physical condition should produce proportionately more sons than mothers in poor condition. Because mothers in good condition are expected to be dominant, several studies of ungulates compared maternal dominance to offspring sex ratio (Clutton-Brock et al. 1984; Festa-Bianchet 1991; Cassinello 1996; Byers 1997; Kruuk et al. 1999; Côté & Festa-Bianchet 2001), with inconsistent results.

Bennett (1986) described dominance relationships among bighorn ewes in captivity. Three earlier studies investigated the dominance hierarchy of bighorn ewes in the wild, but none had information on age, body mass and horn size of marked individuals. Eccles & Shackleton (1986) found a nonlinear hierarchy unrelated to mass or horn length in captive ewes of unknown age. Hass (1991) found an age-related linear hierarchy in a population in which age was known only for ewes younger than 7 years. Festa-Bianchet (1991) used a modification of the index of Clutton-Brock et al. (1986) to determine rank and found that the older ewe won 92% of interactions among ewes of different ages where a winner could be identified. His method to assess rank assumed that normally the older ewe should win all interactions and did not take into account the actual number of interactions won by each member of a dyad (Gammel et al. 2003). In addition, Festa-Bianchet (1991) had no information on ewe body mass or horn length.

The long-term study of marked bighorn sheep on Ram Mountain, Alberta, Canada, provided the opportunity to compare ewe dominance rank with repeated measurements of mass and horn size on each individual and with reproductive success (Festa-Bianchet et al. 1998). Here, we identify the determinants of ewe dominance using path analysis to distinguish the effects of age, body mass and horn size. We predicted that age and body mass should explain most of the variance in rank among ewes. When the establishment of dominance is costly, changes in social rank over time should depend more on traits that can vary annually according to body condition than on traits that are independent of changes in condition. Consequently, although ewes use their horns to interact, we predicted that horn size would have a weak effect on rank. Unlike body mass, which can vary yearly according to condition, the horns of ewes nearly stop growing at about

6 years of age and are therefore a fixed trait for each adult individual. We then examined the consequences of social rank on reproductive success. Because bighorn sheep fit all assumptions of the Trivers–Willard model (Blanchard et al. 2005), dominant ewes should have a male-biased offspring sex ratio. Finally, based on previous studies on bighorn sheep (Eccles & Shackleton 1986; Festa-Bianchet 1991; Hass 1991), we expected that reproductive success would be mostly independent of maternal social status.

METHODS

Study Area and Population

The study population inhabits Ram Mountain (52°8′N, 115°8′W, elevation 1082 to 2173 m), Alberta, Canada. Since 1971, sheep on Ram Mountain have been captured in a corral trap baited with salt several times each summer (Jorgenson et al. 1993). We restrained captured ewes manually, blindfolded and hog-tied them and then removed them from the trap for processing. We recorded body mass and horn measurements at each capture. All ewes were marked with coloured collars and were of known age because they were first captured as lambs. We determined reproductive status at each capture by udder examination, with ewes classified as barren or lactating. The handling process took about 10 to 15 min, but because several sheep were caught at each trapping session, individual ewes could spend up to 3 h in the trap. Our experimental protocol was approved by the Université de Sherbrooke Animal Care Committee (Protocol MFB01), which adheres to the guidelines of the Canadian Council on Animal Care. During observations, we classified ewes as lactating if their lamb was alive. We measured yearly reproductive success by lamb survival to weaning and to 1 year of age. In addition, we recorded sex and birth date for each lamb. For lambs captured at least twice, we also calculated summer mass gain rate and mass adjusted to mid-September (Festa-Bianchet et al. 1996). Data on lamb survival to 1 year are available only for 1998 and 2006.

We adjusted mass to 15 September using repeated measurements of the same individual each summer. We used linear mixed models with a restricted maximum likelihood method to adjust mass by fitting a model of mass as a function of date (considering 25 May as day 1; Pelletier et al. 2007). For lambs and yearlings, the relation between date and body mass is linear. For older animals, a square root transformation linearized the relationship between mass and date (Festa-Bianchet et al. 1996). We included ewe identity (as an intercept) and the interaction between ewe identity and date (as a slope representing individual growth rate) as random effects. We fitted separate regression models for each year of study and used the predicted values of individual intercepts and slopes to adjust individual mass to 15 September. Because horn growth is very slow for females and horn tips readily break, we used the measure of the longest horn taken at the last capture of the summer. Horn length increased with age from 2 to 6 years ($t_{32} = 4.51$, $P < 0.001$, $r^2 = 0.41$) but not for older ewes ($t_{50} = 0.478$, $P = 0.63$, $r^2 < 0.01$).

Behavioural Observations

We conducted approximately 500 h of behavioural observations each year from early June to mid-September in 1998, 2006 and 2007. We recorded social interactions among ewes ad libitum (Altmann 1974) at distances of 200 to 800 m using 15−45× spotting scopes. We classified interactions into five types, based on Geist (1971).

(1) Displacement without contact: one ewe makes an abrupt movement towards another, displacing it without physical contact. Typically, the recipient is resting and the initiator, if successful, takes its place.

(2) Front kick: a female raises a front leg and kicks another female, often after an unsuccessful displacement without contact.

(3) Butt: horn blow against the body of another ewe.

(4) Front clash: two ewes clash horns, often with several blows in succession.

(5) Horn rubbing: a subordinate ewe rubs its horns against those of a dominant ewe.

Statistical Analyses

Using all interactions observed we calculated social rank separately for each year, excluding two ewes that died during summer 1998. We assessed the linearity of dominance matrices using Matman 1.1 for Windows (Noldus Information Technology 2003). We calculated the linearity index h' (de Vries 1995), where $h' = 1$ when the hierarchy is perfectly linear, and tested its significance based on 10 000 randomizations (de Vries 1995, 1998). A linear hierarchy implies that if individual A is dominant over B and B is dominant over C, then A is dominant over C. The h' index is based on the Landau index h (Landau 1951), corrected for dyads with unknown relationships. We also calculated an index of directional consistency, the probability that the winner of a new interaction between two individuals is the one that won most earlier interactions. When the hierarchy was linear, the matrix was reorganized, based on 1000 sequential trials, to minimize first the number and then the intensity of inconsistencies (de Vries 1998). An inconsistency involves an individual that wins against a higher-ranked individual and its intensity is the distance between the ranks of the two individuals. To pool years in subsequent analyses, we calculated relative social rank for each ewe each year as suggested by Côté (2000): $1 - (rank/N_i)$, where N_i is the number of ewes observed during year i.

We used confirmatory path analysis (Shipley 2000a) to assess how age and morphological traits interacted to determine social rank. Path analysis tests for causal links between variables based on a hypothetical causal graph in which variables are linked with directed paths. Our hypothetical causal path model assumed that social rank would be influenced by ewe age, body mass and an age*body mass interaction, but not by horn size. We included a free covariance between horn length and body mass to account for age-independent interindividual variation. A free covariance allows two variables to covary without any causal inference about their relationship, so that another nonmeasured variable (e.g. environment, individual

quality, measurement error) may affect them both. We compared our hypothetical model with a 'full' model that included direct causal paths between horn size and social rank and between body mass and social rank. To explore further the implications of the age*body mass interaction on social rank, we compared the determinants of rank for ewes ages 2−6 years (31 observations of year-specific rank from 23 individuals), when mass was highly correlated with age, and for ewes age 7 years and older (52 observations from 45 individuals), for which mass was independent of age (Fig. 1). Although several ewes appeared to reach asymptotic mass at 5 years, splitting the data set at age 5, 6 or 7 did not substantially change the results. We chose the age of 6 years to balance sample sizes of young and old ewes.

Our data have two properties that prevent a standard confirmatory path analysis: first, a hierarchical structure (we observed 16 ewes for more than 1 year); second, in the analysis including all individuals, variables had clear nonlinear relationships (Figs 1, 2). Therefore, we tested the path models using a d-sep test (Shipley 2000b, 2003; Thomas et al. 2007) instead of the usual tests (structural equation modelling) based on the maximum likelihood estimation of a model covariance matrix (Shipley 2000a). This method tests for the independence relations among variables predicted by models based on the concept of d-separation and can accommodate hierarchical data with particular structural functions and correlated errors (Shipley 2003). In a causal graph, the d-separation concept (Pearl 1998) gives the necessary and sufficient conditions for two variables to be independent upon conditioning on a set of other variables. Based on our hypothetical causal graph, we first determined a basis set of k mutually independent statements of conditional probabilistic independence (d-separation statements) that must be true if the causal model is true (Shipley's basis set). The basis set includes the unique pairs of variables without a direct link ('nonadjacent variables'), in which each pair is conditioned on the direct causes ('causal parents') of each variable of the pair (for details about the d-separation basis set see Shipley 2000a, b). Then, we assessed
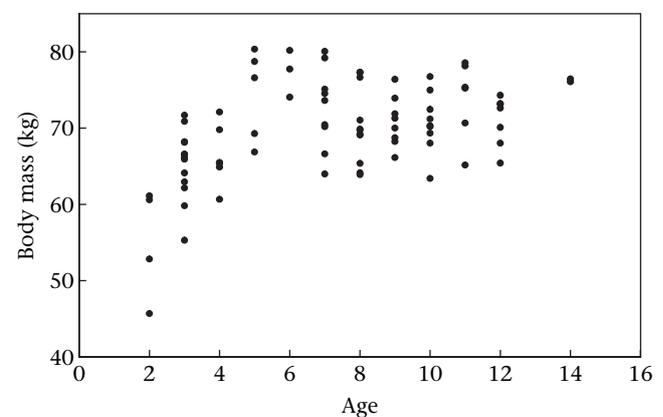

Figure 1. Body mass adjusted to mid-September for 64 adult bighorn ewes (83 ewe-years) at Ram Mountain, Alberta, Canada, in 1998, 2006 and 2007.
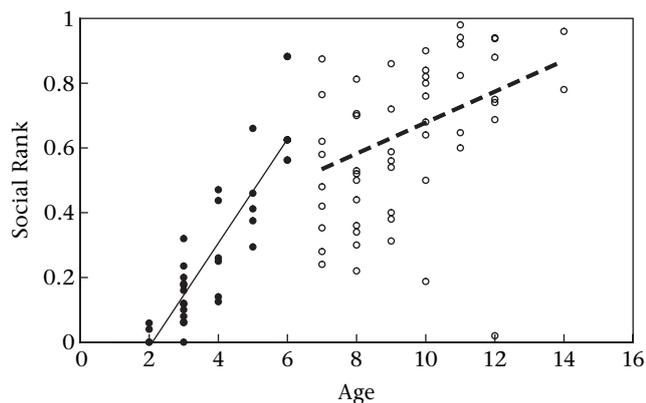
Figure 2. The quadratic relationship of age and social rank for bighorn ewes at Ram Mountain in 1998, 2006 and 2007, decomposed into two linear regressions according to age class. The solid line and black symbols represent ewes ages 2–6 years (31 observations of yearly rank from 23 individuals, $r^2 = 0.75$), the dotted line with open symbols indicates older ewes (52 observations from 45 individuals, $r^2 = 0.15$).

separately the probability of each conditional independence statement of the basis set. Finally, we evaluated if the data fit the path model using Fisher's C test (Shipley 2000a, b). C is defined by $C = -2 \Sigma \ln (p_i)$, where p_i is the probability of each independence statement. C follows a chi-square distribution with $2k$ degrees of freedom (Shipley 2000a, b). The null hypothesis of the Fisher C test is that conditional independence claims are respected. A nonsignificant C value means that the observed and predicted patterns are not statistically different, therefore the data fit the model (Shipley 2000a, b). A significant value would indicate that the model's fit is inadequate (Shipley 2000a, b). Path analysis results are reported as recommended by Shipley (2000a).

We tested the hypotheses of conditional independence predicted by the basis sets of our hypothetical-path models using linear mixed models including ewe identification and year as random effects to account for repeated measures. If the path model predicted an independence of two variables (X, Y), conditional on a set of variables (Z_1, Z_2), noted $X\_\|\_Y \{Z_1, Z_2\}$, we tested this independence by fitting a generalized linear mixed model whose fixed component was $Y \sim Z_1 + Z_2 + X$ and calculated the probability that the partial slope for X was 0 using a t test. When variables had nonlinear relationships (Figs 1, 2), we included quadratic terms in tests of conditional independence. We tested the combined null hypothesis that the partial slopes associated with both the linear and the quadratic term were 0 by calculating F as the ratio of the mean sum of square of the combined quadratic terms and the residual sum of squares of the random effects.

To assess the influence of maternal rank on lamb survival to weaning and to 1 year, parturition date, lamb sex, lamb summer growth rate and lamb mass at weaning, we used mixed models that included ewe identity and year as random effects. In models of lamb survival, we fitted as fixed effects the maternal rank, age, mass at weaning and in mid-September the previous year and the lamb mass at weaning. For analyses of lamb sex and birth date, we

included the maternal rank, age, mass in mid-September the previous year and previous reproductive success. Finally, for lamb growth rate and lamb mass at weaning, we included maternal rank, age, mass in mid-September and lamb sex as fixed effects. For binary response variables (lamb sex and survival), we used a binomial distribution with a logit link function in the mixed model. All statistical analyses used R 2.6.1 (R Development Core Team 2007).

RESULTS

Dominance Hierarchy

Of 1207 interactions observed (Table 1), the most common were displacement without contact (48%) and butt (36%). Front clash was less frequent (14%) and front kick and horn rubbing were rare (3% each). Bighorn ewes formed a linear hierarchy and in all years the outcome of repeated interactions within a dyad was highly consistent (directional consistency index 0.92–0.99; Table 1). Because we observed a smaller proportion of dyads interacting in 1998, the linearity index corrected for unknown dyads, h', was weaker than in 2006 and 2007.

Determinants of Dominance

Hypothetical-path models (HPM; models including only solid lines in Fig. 4) provided a good fit to the data (Table 2). Full-path models (FPM; models including solid and dotted lines in Fig. 4) did not significantly improve the fit (likelihood ratio tests between FPM and HPM: Model A: $\chi^2_4 = 1.95$, $P = 0.74$; Model B: $\chi^2_2 = 0.27$, $P = 0.88$; Model C: $\chi^2_2 = 1.24$, $P = 0.54$). Path models suggested that social rank was determined by age and body mass, whose importance varied according to ewe age and was independent of horn size (Table 2, Fig. 4). Rank increased with age (Figs 2, 4b), but the age–rank correlation was weaker for ewes 7 years and older than for ewes ages 2 to 6 years (Figs 2, 4c). After correcting for age, mass had a strong effect on dominance rank for females 7 years and older (Figs 3b, 4c) but not for younger ewes (Figs 3b, 4b). There was more variability in mass than in horn length: after correcting for age (leading to a mean of 0), the standard deviation of body mass (5.57) was almost twice that of horn size (2.96).

Table 1. Linearity and consistency of the dominance hierarchy of individually marked bighorn sheep ewes at Ram Mountain, Alberta, Canada, in 1998, 2006 and 2007

Year	Females (N)	Interactions observed	% dyads observed	h'*	P†	DC‡
1998	50	629	33.1	0.12	<0.001	0.92
2006	17	375	83.8	0.61	<0.001	0.93
2007	16	203	48.3	0.44	<0.001	0.99

*Linearity index.
†P value of the test for linearity of the h' index.
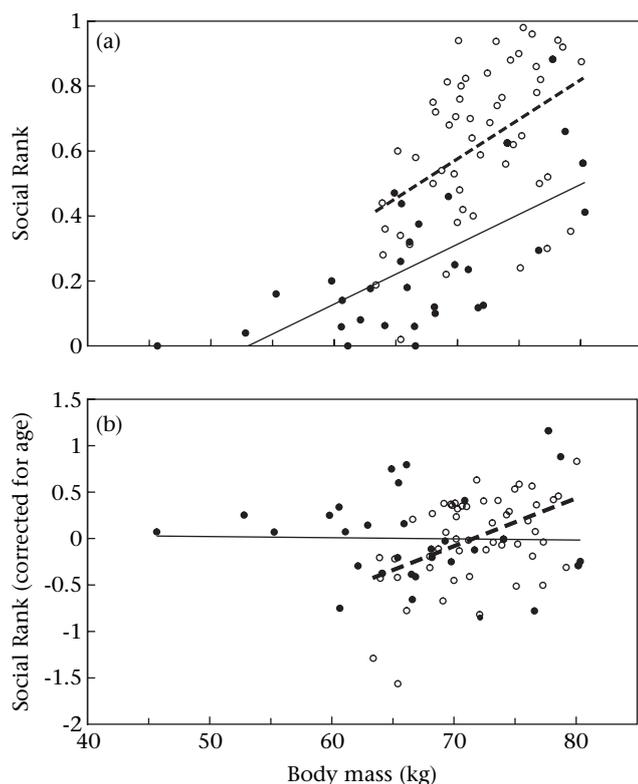‡Directional consistency index.

Figure 3. Body mass adjusted to mid-September and social rank in bighorn ewes at Ram Mountain in 1998, 2006 and 2007. (a) Raw data and (b) rank corrected for age. Solid line and black symbols represent ewes ages 2−6 years (31 observations from 23 individuals, $r^2 = 0.43$ in a and $r^2 < 0.01$ in b). The dotted line and open symbols indicate ewes $\geq$7 years (52 observations from 45 individuals, $r^2 = 0.22$ in a and $r^2 = 0.23$ in b).

Dominance and Reproductive Traits

The only variable that affected lamb survival was maternal mass in mid-September before conception, which had a positive effect (to weaning: $Z = 3.14$, $P < 0.001$, $N = 72$; to 1 year: $Z = 2.10$, $P = 0.03$, $N = 57$). Lamb mass gain rate and mass at weaning increased with maternal mass in summer (mass gain rate: estimate 0.01, $t_4 = 4.46$, $P < 0.01$, $N = 44$; mass at weaning: estimate 0.45, $t_4 = 4.49$, $P < 0.01$, $N = 44$). Male lambs gained mass faster and were heavier at weaning than females (mass gain rate: estimate 0.02, $t_4 = 3.84$, $P < 0.01$, $N = 44$; mass at weaning: estimate 3.08, $t_4 = 3.26$, $P = 0.01$, $N = 44$). None of the variables we examined affected lamb sex (estimate $\pm$ SE: maternal age: -0.17 ± 0.15; social rank: -0.50 ± 1.88; mass before conception: 0.02 ± 0.07; previous reproductive success: 0.01 ± 0.64; $N = 42$; negative estimates indicate a greater (but nonsignificant) probability of producing a female) or birth date (estimate $\pm$ SE: maternal age: -0.03 ± 0.81; rank: 14.56 ± 10.94; mass before conception: -0.56 ± 0.35; previous reproductive success: 2.43 ± 2.88; $N = 42$). Social rank was not related to any of the reproductive traits we considered ($P > 0.10$).

Table 2. Tests of conditional independence in the basis sets implied by the hypothetical-path models in Fig. 4 (solid arrows only) for the relationship between morphology and social rank in bighorn ewes

Basis set	Partial slopes (SE)	F value	Null probability
Fig. 4a, All ewes			
$B\_\|\|\_D \mid \{A, C\}$		$1.93_{2,64}$	0.16
$D \sim A + C + C^2 + (B + B^2)$			
B	-13.9 (6.69)		
B^2	0.28 (0.13)		
$B\_\|\|\_E \mid \{A, D\}$		$0.17_{2,64}$	0.84
$E \sim A + A^2 + E + (B + B^2)$			
B	0.04 (0.06)		
B^2	-0.01 (0.01)		
$C\_\|\|\_E \mid \{A, D\}$		$0.82_{2,64}$	0.45
$E \sim A + A^2 + D + (C + C^2)$			
C	0.07 (0.04)		
C^2	-0.01 (0.01)		
	Partial r	t value	
Fig. 4b, ewes <7 years of age			
$B\_\|\|\_E \mid \{A\}$	0.16	1.19_6	0.23
$C\_\|\|\_E \mid \{A\}$	0.06	-0.16_6	0.88
Fig. 4c, ewes $\geq$7 years of age			
$A\_\|\|\_B \mid \{ \}$	0.22	1.64_6	0.15
$A\_\|\|\_C \mid \{ \}$	0.09	0.65_6	0.54
$B\_\|\|\_E \mid \{A, C\}$	0.01	-0.12_4	0.90

Variables are as follows: age (A), horn length (B), body mass (C), age*body mass interaction (D) and social rank (E). The notation for a conditional independence statement, $B\_\|\|\_D \mid \{A, C\}$, means that variables B and D are independent of each other conditional on both A and C. Conditional independence was evaluated using a combined F statistic (see Methods) for quadratic relations and t test for linear ones. Individual identity and year were added as random effects in all tests of conditional independence. With each d-separation statement involving polynomial terms, we present the fixed part of the model used to evaluate conditional independence. The causal models provide a good fit to the data as indicated by the P value of the C test (model in Fig. 4a: $\chi^2_6 = 5.7$, $P = 0.47$; Fig. 4b: $\chi^2_4 = 3.23$, $P = 0.5$; Fig. 4c: $\chi^2_6 = 5.18$, $P = 0.5$).

DISCUSSION

We found stable and linear dominance hierarchies among bighorn ewes. Individual rank increased with both age and body mass, but the positive effect of age on social rank appeared weaker than reported by other studies of female ungulates (Thouless & Guinness 1986; Hass 1991; Festa-Bianchet 1991; Côté 2000 reported rank−age correlations between 0.6 and 0.96). Once age was accounted for, ewe dominance increased with body mass but not with horn size. Maternal dominance rank, however, did not affect lamb birth date, mass, growth, survival or sex ratio.

The large difference in linearity index between years (Table 1) arises mostly because many dyads were not seen to interact in 1998, when many more ewes were under observation. Despite these differences, h' was significant in all years. The directional consistency index was always very high, suggesting that established dyadic relationships were respected in subsequent interactions, leading to a stable social hierarchy in each year. The correlation between ranks of the same 16 ewes in 2006 and 2007 ($r = 0.83$)
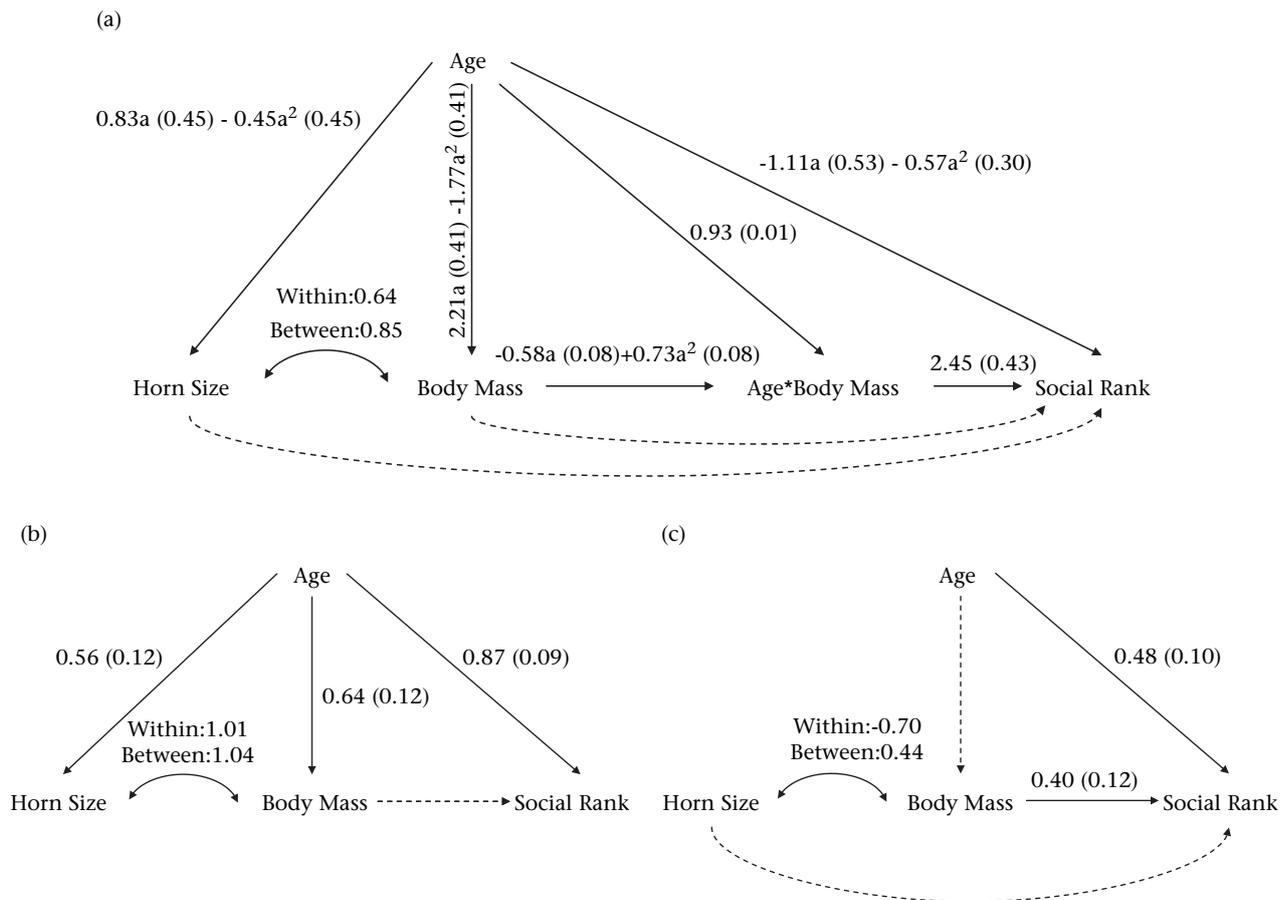
(a)

(b)

(c)

Figure 4. Path analyses of the determinant of social rank in bighorn ewes on Ram Mountain. (a) All females (83 observations of 64 individuals), (b) ewes <7 years of age (33 observations of 23 individuals) and (c) ewes ≥7 years of age (50 observations of 45 individuals). Significant causal paths are shown in bold with their standardized path coefficients. Dotted arrows indicate nonsignificant paths tested in the full models. 'Within' and 'between' refer to within and between individual covariance of horn size and body mass.

suggests that the hierarchy is mostly stable over time, but some changes occur. More years of observations are required to quantify stability in social rank. Other studies of ungulates found stable linear hierarchies in both sexes (Locati & Lovari 1991; Greenberg-Cohen et al. 1994; Côté 2000; Pelletier & Festa-Bianchet 2006).

Consistent with several other studies of female ungulates (Festa-Bianchet 1991; Hass 1991; Greenberg-Cohen et al. 1994; Côté 2000), we found a strong effect of age on social rank. However, the correlation of age and rank weakened after ewes reached asymptotic mass at 7 years (Festa-Bianchet et al. 1996). Our results are remarkably similar to those obtained for bighorn rams by Pelletier & Festa-Bianchet (2006): for young sheep, age plays an important role in social rank, probably because at 2−6 years of age, the older sheep is usually heavier. Because of the correlation between age and mass for younger ewes, however, once age is included in the analysis, mass does not explain any further variance in rank. After asymptotic mass is reached, differences in body mass among individuals are mostly independent of age and become the predominant factor determining dominance. The age-related change in the relationship between mass and social rank implies that fully grown ewes assert their

dominance status over older (but lighter) ewes to which they were previously subordinate. As predicted, we found no effect of horn length on social dominance. Horn size for adult bighorn ewes is a fixed trait that mostly depends on horn growth over the first 4 years of life and is independent of yearly changes in body condition. The low variance in horn size once corrected for age decreases the statistical power to detect a possible effect on dominance.

For rams, dominance involves substantial fitness benefits. Only the most dominant rams can use the highly successful mating strategy of tending oestrous females (Hogg & Forbes 1997). Our finding of a similar relationship between age, mass and dominance in females suggests that ewes also gain a benefit from being dominant, but it is unclear what that benefit may be. There are no data suggesting that access to males during the rut is related to ewe dominance, and we found no fitness correlates of ewe dominance rank. Although bighorn sheep fit all the assumptions of the Trivers−Willard model (Hogg et al. 1992; Bérubé et al. 1996), they show no effect of social rank on offspring sex ratio (Festa-Bianchet 1991; Blanchard et al. 2005). Blanchard et al. (2005) suggested that the Trivers−Willard model requires a strong relationship between dominance and reproductive success. In bighorn

ewes, we found neither a strong relationship between social dominance and reproductive success nor support for the Trivers–Willard model.

Social status may play an important role during harsh winters with deep snow. When ewes must dig craters to reach forage covered by snow, dominant females may evict subordinates from snow craters, as observed in caribou, *Rangifer tarandus*, and reindeer (Barrette & Vandal 1986; Holand et al. 2004b). Bighorn sheep generally winter in areas with limited snow cover so that in most years competition over snow craters may occur on only a few days. In winters with deep snow, however, that competition could affect individual body reserves and subsequent reproductive success (Festa-Bianchet 1998).

Individual-level data on rank, age, body mass and reproductive performance over several years combined with path analysis provide a promising avenue to assess the determinants and consequences of social rank in wild populations. For bighorn ewes, neither the advantages of being dominant nor the potential costs of dominance are well understood. Longer-term monitoring of social status, changes in body mass and life-history characteristics is required to identify the costs and benefits of being dominant. The social hierarchy of adult bighorn ewes on Ram Mountain appeared less strongly affected by age than that of female ungulates in other populations. Presumably, fully grown ewes spend some energy challenging older individuals to reverse previously established rank relationships, suggesting that there are advantages in being dominant.

Acknowledgments

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