



## Dominance, fatness and fitness in female American bison, *Bison bison*

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In females of several mammalian species, it is becoming evident that benefits related to high dominance rank can result in increased fitness, albeit to a lesser degree than in males. We examined indicators of fitness in relation to dominance rank in a group of adult female American bison in semifree-ranging conditions. A significantly linear dominance hierarchy was found. Dominance rank correlated significantly with three indicators of body condition: weight, speed of hair loss and fatness. After statistical correction for the other two factors, only the link between rank and fatness remained significant. Dominant females did not show higher fecundity, nor did their daughters. Combining the results over the study years, we found that weight of offspring at weaning correlated significantly with maternal rank.

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Females have been considered to be less sexually strategic than males because they gain relatively less from competitive reproductive tactics (Hrdy 1999). Although in general variance in reproductive success is lower in female mammals than in males, it is becoming increasingly evident that selection has shaped competitive behaviour and the formation of dominance hierarchies in females (Hrdy & Williams 1983). In several ungulate species, female dominance relationships are linearly organized (bison: Rutberg 1986; red deer, *Cervus elaphus*: Thouless & Guinness 1986; reindeer, *Rangifer tarandus*: Hirotani 1990; bighorn sheep, *Ovis canadensis*: Festa-Bianchet 1991; Hass 1991; gazelles, *Gazella dama*, *G. cuvieri*: Alados & Escos 1992; sable antelope, *Hippotragus niger*: Thompson 1993; Icelandic horses, *Equus caballus*: Van Dierendonck et al. 1995; mountain goats, *Orlamnos americanus*: Côté 2000). Evidence that such dominance relations among female mammals also influence their fitness is scarce yet compelling (Pusey et al. 1997; von Holst et al. 2002).

Female fitness is affected not only by the quantity of calves produced, but also by qualitative differences that affect offspring survival and reproduction. An important

qualitative factor is weight of the offspring. Male weight can be a reasonable predictor for subsequent reproductive success (e.g. bighorn sheep: Festa-Bianchet et al. 2000). In females it is well documented that reduced weight may reduce fertility (red deer: Loudon et al. 1983), delay onset of reproduction (humans: Reid & Van Vugt 1987) or prolong lactational infertility (rats, *Rattus norvegicus*: Woodside et al. 1998). One factor influencing offspring weight at weaning is the timing of birth. The benefits of giving birth early in the season are increased mass of the offspring (reindeer: Holand et al. 2003), increased calf survival (bighorn sheep: Festa-Bianchet 1988; red deer: Loison et al. 1999) and higher dominance (bison: Green & Rothstein 1993). Delayed calving is related to reduced future fertility of the mother (red deer: Clutton-Brock et al. 1987; caribou, *Rangifer tarandus*: Cameron et al. 1993). Late-born daughters reproduce later (red deer: Langvatn et al. 1996), mature later and have lower fecundity (bison: Green 1987; Green & Rothstein 1993).

Depending on the ecological circumstances, variance in the reproductive success of female bison can be high in some years (Appendix). Presumed causes of variance in reproductive success include periods of poor food intake resulting in poor condition (Del Giudice et al. 2001) and deferred reproduction (ungulates: Geist 1971; Belonje & Von Niekirk 1975; Sinclair 1977; bison: Berger & Cunningham 1994), disease (brucellosis in bison: Thorne et al. 1989; parasites in bison: Rutley et al. 1997; tuberculosis in bison: Joly 2001) or an age-related tendency to

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skip births resulting in stochastic oscillations (bison: Green & Rothstein 1991a; Kirkpatrick et al. 1993). Other factors being equal, bison herds with a 1:10 mature male:female ratio, as is common in commercial herds, show similar birth rates as herds with a 1:1 ratio (Rutley et al. 1997). Overall, variance in the reproductive success of females is similar for wild and captive conditions, although the full reproductive potential with all females of a herd giving birth is never reached in wild conditions. Farmed or semi-free ranging bison do not experience the severe food deprivation that occurs in free-ranging herds (e.g. Lott & Galland 1987). Nevertheless, even in farmed bison the pregnancy rate can drop as low as 37.5% (Rutley et al. 1997). Green (1987) found that dominant young and prime-aged bison females were more fecund than their peers. In ungulates, there is a relation between an adult female's mass and her probability of reaching old age, thus indirectly positively affecting her lifetime individual fitness (Gaillard et al. 2000).

We aimed to study the effects of dominance on female fitness in a captive herd of American bison. The captive setting has obvious benefits and drawbacks. Given the restricted spatial range and good individual recognition, coverage of a large percentage of the dyadic dominance relationships is feasible. A disadvantage is that the variation in number of calves produced can be expected to be low. Commercial herds, as well as public herds in which herd size, pasture rotation and parasite load are controlled, indeed show higher fecundity than nonmanaged free-ranging bison (Rutley et al. 1997). A benefit of working on captive animals is that life history data can be thoroughly quantified for the entire herd. Age explains 90% of the variance in female social dominance rank in mountain goats (Côté 2000) and is an important determinant of rank in female bison (Rutberg 1983, 1986; but see Lott & Galland 1987) and red deer (Thouless & Guinness 1986). Furthermore, age is an important source of individual variation in reproductive success in bison (Green & Rothstein 1991b; Berger & Cunningham 1994, page 146). Since all our study females were mature and of the same age we could study dominance rank independently from age.

We first analysed the linear rank order in the herd (De Vries 1995, 1998) and then related dominance rank to indicators of female quality: body weight, fatness and speed of hair loss. We also investigated the link between dominance and the observed reproductive success itself (fecundity), the inclusive fitness (daughters' fecundity) and offspring quality (weight of offspring) throughout several years. We predicted that high-ranking females would be more fecund, have more fecund daughters and have heavier offspring.

## METHODS

### The Study Herd

The study herd was composed of 42 mature female American bison, grazing year-round on pastures of 20 ha on average in a rotation system with two other herds

(200 ha total) on a commercial farm in the Belgian Ardennes. Grass was plentiful in summer and hay was continuously provided ad libitum from October to April. Snow cover periods occurred between November and February. Hay was provided at a feeder accessible by about 10 individuals at a time. In June, the adult breeding males joined the herd with a ratio of one male per 10 females and remained there until October. Calves were weaned in December at about 7 months of age and removed from the herd. Management involved one yearly roundup in winter for vermifugation, health checks, weighing and weaning of calves, and a summer roundup for ear labelling and vermifugation of newborn calves. All individuals were labelled with eartags. Three females were born in 1991 and the others ( $N = 39$ ) were born in 1992. All were kept in the same group of initially 60 individuals in 1993 from which 18 individuals were sold, culled, or died.

### Observation Method and Period

In 2001, we carried out observations between 26 May and 14 September during 325 h. In 2002, the herd was observed between 27 May and 27 September during 456 h. The animals were observed from a  $4 \times 4$  vehicle within the herd and were habituated to its presence. All agonistic behaviours (see ethogram) were scored ad libitum. To ensure equal observation of all individuals, the observer switched position every 30 min to cover front, mid and back positions of the herd.

### Ethogram of Agonistic Behaviours

#### Aggressive behaviours

- (1) Displacement: approaching within one body length whereupon another individual yields.
- (2) Threat low: lowering the head towards an opponent.
- (3) Threat nod: nodding the head towards an opponent.
- (4) Threat swing head: swinging the head towards an opponent.
- (5) Threat lunge: brisk brief movement in the direction of another individual, accompanied by lowering, nodding or swinging the head.
- (6) Brief (long) chase: run after fleeing individual for less (more) than two body lengths.
- (7) Thrust horn: strong contact with the horn on or in the body of another individual.
- (8) Butt: lowering the head and butting another individual.
- (9) Fight: repeated butting and forward pushing against the other individual with lunges.
- (10) Kick: kicking with hindlegs towards an individual.

#### Submissive behaviours

- (1) Walk away, jump away or flee: walk away, jump or run away at least one body length upon approach of other individual within one body length.
- (2) Avoid: start walking away from approaching individual well before it is within one body length.

## Dominance Rank Analysis

To determine the dyadic dominance relationships we used all possible aggressive behaviours followed by a submissive behaviour (Vervaecke et al. 2000). Since there were tied or unknown relationships, the improved index of linearity ( $h'$ ) rather than Landau's index was calculated and tested by means of a randomization test with the aid of MatMan (De Vries 1995). Since the degree of linearity was highly significant, the dominance matrix was reordered to find an order most consistent with a linear hierarchy by the I&SI method which minimizes the number of inconsistencies and the strength of inconsistencies (De Vries 1998; MatMan software: De Vries et al. 1993). In the linear rank order, the top individual is assigned rank 1 and the lowest-ranking individual rank  $n$ . The directional consistency index (DC) gives the frequency with which the behaviour occurred in its more frequent direction relative to the total number of times the behaviour occurred (Van Hooff & Wensing 1987). The total number of times the behaviour occurred in the direction of the higher frequency ( $H$ ) minus the number of times in the less frequent direction ( $L$ ) is divided by the total frequency  $DC = (H - L)/(H + L)$ . The number of one-way relationships describes the number of dyads in which the behaviour is shown in one direction only, regardless of the frequency of interaction within the dyads. In two-way relationships, dyadic dominance interactions occurred at least once in both directions (from A to B and from B to A). Thoroughly substantiated rank data were obtained in 2001 and 2002. Since the ranks were strongly correlated between adjacent years (2001–2002:  $r_s = 0.782$ ,  $N = 41$ ,  $P < 0.0001$ ), and since Rutberg (1983) noted that hierarchies in bison cows seem to be established at an early age and not contested later, we used the rank data of 2001 to investigate fitness effects (correlation between rank, weight, birthdates, weight of offspring) in the preceding years (2000, 1999). Thus, for this period ranks were inferred and these correlations must therefore be interpreted with caution.

## Estimates of Body Condition: Hair Loss, Fatness

Bison lose the winter robe in patches and the area of uncovered skin increases as moulting proceeds, giving a range of values of 0–100%. We monitored the degree of hair loss and fatness for the entire herd on 6 June. After checking the herd, we made a second evaluation in the reverse order to correct for fluctuation of observers' criteria during the evaluation.

Fatness was evaluated on 6 June on a scale from 5 to 1: 5 = clear fat deposit on croup and around tail base, no ribs visible; 4 = no ribs visible, some fat deposit around tail base; 3 = no fat deposit, no ribs visible; 2 = tail in a socket, ribs slightly visible; 1 = tail in deep socket, ribs clearly visible. In case of difficulty of assigning a state to an individual, e.g. either 2 or 3, the midpoint was noted: 2.5.

## Weights, Fecundity and Birthdates

Weights of breeding females and dependent calves were obtained yearly in winter, except in 2000. Occasionally, an individual could not be weighed because of handling difficulties. Fecundity was defined as the number of births per year. Data on fecundity of daughters were available for a limited number of females born in 1998 that remained on the farm in a different herd. Birthdates were scored daily for all females since 1999.

## Other Analyses

We performed normality analyses (Kolmogorov–Smirnov tests) prior to applying appropriate statistical tests, with the SPSS software (SPSS Inc., Chicago, IL, U.S.A.). All reported  $P$  values are two tailed. We used nonparametric statistics when normality and/or homogeneity of variances was not satisfied. We used Spearman rank correlation to correlate dominance rank with individual attributes. Since barren females did not invest in gestation, their condition and weight are superior at the end of the year (Green & Rothstein 1991b) and they can be expected to show earlier hair loss and resume oestrus earlier. Therefore, when correlating rank with robe loss, weight of mother or calf, or birthdate, we excluded females that had been barren in that year (6 in 1999; 2 in 2000; 4 in 2001; 3 in 2002) or the preceding year. A female that had twins (in 2000) was also excluded.

When correlating maternal rank or weight with offspring weight or birthdate, we tested the same hypothesis on sets of data gathered in 4 different years. The data were not pooled since they were not balanced (owing to different offspring of sexes, some barren years for some females, slightly different dominance ranks in 2001 and 2002) but the test outcomes of different years were combined in a Fisher combination test (Sokal & Rohlf 1981, page 780). If the null hypothesis is true, the quantity  $-2\sum \ln P$  is expected to be distributed as  $\chi^2$  with degrees of freedom = 2 times the number of separate tests. A value of  $-2\sum \ln P$  greater than the corresponding  $\chi^2$  value allows us to reject the null hypothesis of no effect. We used a Bonferroni-corrected critical significance level to correct for the familywise error rate when a family of related tests was performed (Chandler 1995).

## RESULTS

### Dominance Hierarchy Analysis

Table 1 presents the results of the dominance analyses. For 2001, the dominance relationship was expressed by at least one interaction for 72.11% of the total relationships. The ensuing linearity index corrected for unknown relationships  $h'$  equalled 0.52 and was highly significant ( $P < 0.0001$ ). For 2002, the dominance relationship was expressed by at least one interaction in 75.85% of the total relationships. The  $h'$  was 0.53 ( $P < 0.0001$ ). A top-ranking female of 2001 dropped to the lowest position the subsequent year, after she lost both horns in a fight with another female. For the other females, ranks between years did not differ much.

**Table 1.** Analysis of linearity of the hierarchy in 2001 and 2002

	2001	2002
Matrix total	1810	1941
Linearity index $h'$ (corrected for unknown relationships)	0.524***	0.530***
Expected value of $h'$	0.070	0.071
Directional consistency index	0.947	0.933
Number (%) of unknown relationships	193 (22.42)	140 (17.07)
Number (%) of one-way relationships	625 (72.71)	622 (75.85)
Number (%) of two-way relationships	42 (4.88)	58 (7.07)
Total number of dyads	860 (100)	820 (100)
Number (%) of tied relationships	9 (1.05)	20 (2.44)

\*\*\* $P < 0.0001$  with the improved linearity test (De Vries 1998).

### Correlation of Rank with Body Condition

Weight, degree of hair loss and in particular fatness correlated significantly with female rank (Table 2). Only the partial correlation between fatness and rank remained significant when we controlled for both other factors. Of the body condition parameters, fatness is clearly the one that correlated strongest with dominance rank.

### Correlation of Rank with Fitness Indicators

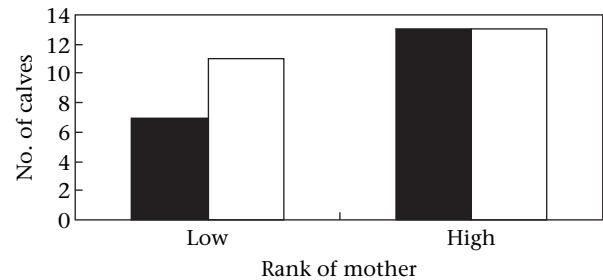
#### Fecundity

There was little variation in the proportion of females that had a calf (Fig. 1). On average 93.4% (range 89–100%) of the females calved. We found no significant correlation between female rank as measured in 2001 and her lifetime fecundity from age 3 ( $r_s = -0.104$ ,  $N = 30$ ,  $P = 0.584$ ).

**Table 2.** Spearman correlation ( $r_s$ ) of dominance rank with estimates of body condition in female bison in 2001

	$r_s$	df
Rank–hair loss	-0.38*	38
Rank–fatness	-0.63***	38
Rank–weight	-0.35*	38
Hair loss–fatness	0.35*	38
Weight–fatness	0.44**	38
Weight–hair loss	0.39*	38
Rank–hair loss, fatness controlled	-0.24	35
Rank–fatness, weight controlled	-0.57***	33
Rank–fatness, hair loss controlled	-0.58***	35
Rank–weight, fatness controlled	-0.16	33
Hair loss–fatness, rank controlled	0.09	35
Weight–fatness, rank controlled	0.23	33
Weight–hair loss, rank controlled	0.07	33

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ , all two tailed. With a Bonferroni-adjusted critical significance level of 0.004 (= 0.05/12) only the \*\*\*-marked correlations are significant. Since high-ranking females have a low ordinal rank number, the correlations with rank are negative.

**Figure 1.** Number of calves surviving (□) and number born (■) for daughters of low-ranking and high-ranking bison females in their first 2 breeding years.  $N = 8$  for both low- and high-ranking females.

#### Fecundity of daughters

Daughters of high-ranking mothers were not more fecund than daughters of low-ranking mothers (percentage of calves born in 2001 and 2002 to daughters of high-ranking mothers: 46%; low-ranking mothers: 54%, binomial test:  $P = 0.84$ ; calves surviving for daughters of high-ranking mothers: 35%; 65%; binomial test: low-ranking mothers:  $P = 0.26$ ) (Fig. 1).

#### Weight of offspring

The correlation between maternal rank and daughter's weight (Table 3) was masked by the correlation between maternal weight and daughter's weight. When the latter was controlled for, a significant correlation appeared. So, after taking into account the fact that heavy mothers produced heavy daughters, we found that high-ranking mothers produced heavy daughters. High-ranking females may give birth earlier. However, when we controlled for birthdate the correlation between rank of mother and weight of daughter at weaning hardly changed (Table 3).

When we considered the combined test result of the different years, maternal rank and son's weight at weaning correlated significantly (Table 3). This association could be a side-effect of the facts that higher-ranking mothers are heavier and that heavy mothers produce heavy sons. The loss of significance after correction for this third factor confirms this (Table 3). High-ranking females may give birth earlier and therefore produce heavier sons. Here, ambivalent results were obtained. In one year the correlation increased after we controlled for birthdate but in three other years it decreased (Table 3). When we combined these yearly outcomes in a Fisher combination test a  $P$  value of 0.016 resulted, which is not significant when applying a Bonferroni correction.

## DISCUSSION

### Dominance Rank and Individual Attributes

Weight is generally used as a reliable indicator of female quality. We found a significant correlation between rank and weight, confirming previous bison studies (Lott & Galland 1987; Green & Rothstein 1991a; but not Rutberg 1983). For this association, two causal explanations can be suggested: weight may affect fighting ability and thus



**Table 3.** Spearman rank correlations ( $r_s$ ) between maternal rank and maternal weight and offspring weight at weaning

Correlation with	1999 (rank 2001)	2000 (rank 2001)	2001 (rank 2001)	2002 (rank 2002)	Fisher Combination test		
					$-2\sum \ln P$	<i>df</i>	<i>P</i>
Mother's weight	-0.38 (39)	NA	-0.35 (36)	-0.30 (35)	19.31	6	0.003*
Daughter's weight	-0.50 (17)	-0.35 (9)	-0.38 (13)	-0.35 (15)	14.79	8	0.063
Daughter's weight (controlled for mother's weight)	-0.71 (15)	NA	-0.68 (13)	-0.01 (15)	19.47	6	0.003*
Daughter's weight (controlled for daughter's birthdate)	-0.53 (13)	-0.54 (6)	-0.22 (10)	-0.42 (12)	15.26	8	0.054
Son's weight	-0.54 (17)	-0.51 (21)	-0.35 (17)	-0.45 (11)	22.39	8	0.004*
Son's weight (controlled for mother's weight)	-0.54 (14)	NA	-0.25 (16)	-0.36 (9)	11.29	6	0.079
Son's weight (controlled for son's birthdate)	-0.50 (14)	-0.57 (18)	-0.16 (16)	-0.35 (9)	18.85	8	0.016

NA = not available. Sample sizes are given in parentheses. The results of 4 (or 3) years were combined in a Fisher Combination test. \*Significant when a Bonferroni-adjusted critical significance level of 0.007 (= 0.05/7) was applied.

result in high rank and/or high rank may improve feeding access and thus ensure high weight. The first line of reasoning assumes that body weight is related to fighting ability. Lott & Galland (1987) suggested that bison groups in which dominance relationships are challenged should show a realignment between rank and weight (as seen in cattle *Bos taurus*: Bouissou 1972). In our group weight indeed reflected fighting ability (frequency of initiated aggression versus weight (2001):  $r_s = 0.321$ ,  $N = 40$ ,  $P = 0.044$ ). The second line of reasoning suggests that the relation between rank and weight in mature bison females is related to differential resource allocation (Green & Rothstein 1991b). Although grass is assumed not to be a contested resource (Lott 2002), Rutberg (1986) showed that dominant bison cows had a higher foraging efficiency during snow cover periods. Low-ranking individuals that had swept away the snow were often displaced without having sufficient time to finish the grass. At our study site, extra hay is provided ad libitum in winter and the quality of grass on the meadows decreases during the nongrowing season. The provisioned food is spatially clustered so that rank-related feeding priority is possible. While the top-ranking females are eating the hay, the lower-ranking animals wait nearby grazing low-quality grass around the stack or scraping snow away to feed. After feeding, the top-ranking animals may block the access or move away to feed or ruminate elsewhere. The others stay behind for only a limited time and quickly resume the herd movement. For female bison, group membership is a strong drive and there is a marked synchrony in activity (Berger & Cunningham 1994; Lott 2002). A low individual tendency for cohesion or a drive to disperse might have been counteracted by predation pressure which can be severe in bison (Lott 2002) or by interfemale aggression upon entering a group. We indeed observed several times in the captive herds that the addition of a new female or a known female re-entering a herd provoked severe female aggression. Thus, the combination of potential intragroup competition, the constraints to leaving a group and the

pressure to synchronize activities may result in differential food intake in group-living grazers, even at relatively low levels of competition, reflected in rank-related differences in body condition. Our study underlines the fact that ample food provisioning in captivity does not automatically result in homogeneous body condition. Holand et al. (2004) found in an experimental herd of reindeer that high-ranking females gained weight during winter, whereas low-ranking ones lost weight. However, free-ranging red deer females did not suffer weight loss from interference competition at artificial feeding sites in winter, and rank and feeding time were correlated only among top-ranking females (Veiberg et al. 2004).

The causal mechanisms of the association between weight and rank may comprise both of the above suggestions. Fatness may actually be a better measure than weight as a condition parameter. Our analysis revealed that weight, fatness and degree of hair loss were all related to rank but the association between rank and fatness was the most robust. The significant correlation between weight and fatness was overridden by their mutual association with rank. Given a similar weight (and age), large but thin females are likely to be lower ranking than small fat individuals. We also observed that possession of horns may be important in rank acquisition and maintenance in bison (as they are in cattle: Bouissou 1972). Over the course of a year, a female dropped from top to bottom rank after losing her horns during a fight with another female.

## Dominance Rank and Fitness

### *Fecundity and daughter's fecundity*

Overall, in our study high female rank was not related to direct and inclusive fitness measures. As expected, the observed variance in reproductive success in the study herd was low. We did not find higher fecundity for high-ranking females, in line with Rutberg's (1986) study. Although in our study maternal condition varied with rank, it apparently did not deteriorate to the degree of

reduced fertility. This may be a consequence of food provisioning. In addition, calves were weaned at a younger age (7 months) than in the wild (between 8 and 20 months: Green 1987) resulting in minimal negative effects on maternal fecundity. We found that the rank of the mother did not correlate with the daughter's fecundity over the first 2 breeding years. Similarly, Green & Rothstein (1991b) found that dominance of the mother was not related to fecundity of daughters, or age at first reproduction of daughters.

### Offspring weight

Maternal rank was correlated with the weight of offspring. A probable causal pathway is that rank determines maternal weight and fatness during conception and gestation, which for a large part determine the offspring's weight at birth. In addition, high maternal rank may mediate a priority of female access to the bull or earlier postbirth resumption of oestrus and early birthdate (as in reindeer: Holand et al. 2004), resulting in a higher offspring weight at weaning. Green & Rothstein (1993) found that for both sexes, early born yearlings ranked higher than their later born peers. Early born individuals, especially females, were larger later in life. Furthermore, mothers that calved early were in better body condition and came into oestrus earlier in the breeding season than late-calving mothers (Berger 1989). Differences in early development are generally assumed to have long-term effects on offspring fitness (Clutton-Brock 1991). Individuals that are large early in life also tend to be large later in life (Cheverud et al. 1983). Green & Rothstein (1991b) found that the yearling body weight of bison was significantly correlated with weight at 3.5 years for sons but not for daughters. From 2 years of age, male bison already participate in contests over female access, although few are successful at this age (Roden et al. 2003). Male weight is strongly related to rank in bison (Roden et al. 2005) and can be considered a reasonable predictor of subsequent reproductive success (e.g. bighorn sheep: Festa-Bianchet et al. 2000). While females may compensate by postponing their first reproduction, males appear not to do so (Festa-Bianchet et al. 2000). It is not unusual for mothers to have a larger impact on the fitness of their sons than on that of their daughters (Clutton-Brock et al. 1982; Clutton-Brock 1991). In horses, sons of high-ranking mothers, which were also mothers in better condition because of superior access to food resources, had higher reproductive success than sons of subordinate mothers (Feh 1990). It is known that in a bison herd with several males present at a ratio of one bull to 10 females, 80% of the females are fertilized by the same bull (Roden et al. 2003). Given the close link between weight, rank, dominance and reproductive success in males, high-ranking females may occasionally get a fitness jackpot by producing a heavy son.

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## Appendix: Variation in Female Reproductive Success in Bison

Study	Variance in reproductive success	Site	Management*
McHugh 1958	Pregnancy rates for ages 2–12; range 78–100%	National Bison Range, Montana, U.S.A.	Free
Fuller 1960	Little more than half the cows conceive each year	Hay Camps Herd, Wood Buffalo National Park, Canada	Free
Fuller 1966	Fecundity 38%	Wood Buffalo National Park, Canada	Free
Meagher 1973	Calving rate of 50% of sexually mature cows	Yellowstone National Park, U.S.A.	Free, harvested beyond boundaries
Haugen 1974	Fecundity 87% for 2-year cohort	Fort Niobrara National Wildlife Refuge (FN) Nebraska & Custer State Park (CSP), South Dakota, U.S.A.	FN: managed by roundups CSP: roundups and harvest
Rutberg 1984	60.4% mature cows with calves	National Bison Range, Montana, U.S.A.	Managed by roundups; culling rate and pasture rotation techniques (fenced subdivisions) similar to commercial (Rutley et al. 1997)
Van Vuren & Bray 1986	63% pregnancy rate	Henry Mountains, Utah, U.S.A.	Free, limited harvest
Lott & Galland 1987	Pregnancy rate of 35% for mature cows	Santa Catalina Island, California, U.S.A.	Free (island), undernourished population (Lott & Galland 1987)
Shaw & Carter 1989	71.8% pregnancy rate	Wichita Mountains Wildlife Refuge	Free, roundups
Green & Rothstein 1991a	Age-specific fecundity range 74% (age 10)–86% (age 7)	Wind Cave National Park, South Dakota, U.S.A.	Free, managed by roundups & culling
Kirkpatrick et al. 1993	Mean 48.2% pregnancy rate; calving rate range 35–55% over 2 years	Mary Mountain & Northern Range herd in Yellowstone National Park, U.S.A.	Free, harvested beyond boundaries Severe nutritional limitations (Berger & Cunningham, 1994, page 119)
Berger & Cunningham 1994	Fecundity 75% for 10–11 year cohort	Badlands National Park, U.S.A. National Bison Range, Montana, U.S.A.	Free, controlled beyond boundaries Managed by roundups; culling rate & pasture rotation techniques (fenced subdivisions) similar to commercial (Rutley et al. 1997)
Kirkpatrick et al. 1996	Mean cow with calf rate for mature females 42.6%	Mary Mountain in Yellowstone National Park, U.S.A.	Free, harvested beyond boundaries Severe nutritional limitations (Berger & Cunningham, 1994, page 119)
Rutley et al. 1997	Pregnancy rate range 37.5–100%, mean 87.0%	16 herds in Peace Country Canada	Commercial herds, provisioned & harvested
Wolfe et al. 1999	Pregnancy rate range 32.5–66.6%, mean 46.2%, > 2-year-old females throughout 10 years	Antelope Island Park, Utah, U.S.A.	Free (island), annual roundup & some culling, poor nutritional plane

\*See Table 2.2, page 40, in Berger &amp; Cunningham (1994) for management practices in bison herds on public lands in Canada and U.S.A.