

# Sociality, Mate Choice, and Timing of Mating in American Bison (*Bison bison*): Effects of Large Males

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Received: April 23, 2007

Initial acceptance: May 26, 2007

Final acceptance: June 30, 2007

(S. K. Sakaluk)

doi: 10.1111/j.1439-0310.2007.01411.x

## Abstract

We studied group size, composition, and mating activities in American bison (*Bison bison*) during rut on the Delta Junction Bison Range in interior Alaska, USA, in 1996 and 1997. Our purpose was to determine the effects of large males ( $\geq 5$  yr old) on mating and associated activities. Groups with large males were larger than those containing smaller males. Most groups of bison were mixed-sex (90%), but large males occurred in only one-half of all groups. Moreover, females in groups with large males were more likely to copulate than those in groups with smaller males, indicating a female preference for large males. Nevertheless, our results are consistent with large males seeking out adult females for mating rather than vice versa. Mating peaked in mid-August during both the study years and was highly synchronous. Scent marking was coincident with mating, an outcome consistent with a hypothesis of such behavior triggering ovulation. Scent marking by large male bison occurred in both male–male and male–female contexts, but was associated most often with sexual activities. No differences in group size occurred with changes in weather or among vegetation types occupied by bison. Group size of bison, however, was larger with increasing distance from the forest edge, which likely was a response to predation risk in this predator-rich environment.

## Introduction

The American bison (*Bison bison*) is a sexually dimorphic ruminant (Berger & Peacock 1988; Weckerly 1998) that exhibits a tending-bond mating system in which older, large-bodied, dominant males typically mate more often than younger, small-bodied subordinates (Lott 1974, 1979, 1981, 1985; Berger & Cunningham 1994). Behavioral evidence of polygynous mating is supported by genetic verification of high variability in reproductive success of male bison, with mature males mating more often than younger individuals (Wilson et al. 2002; Roden et al. 2003). Reproductive success of male bison is greater for prime-age individuals than for younger or senes-

cent animals (Maher & Byers 1987), with prime-aged ungulates often exhibiting a concomitant increase in male effort expended during rut (Bowyer 1981; Mysterud et al. 2004).

Our purpose was to quantify the group size and composition of American bison during rut in relation to environmental and social factors influencing timing and synchrony of mating in a population where large males ( $\geq 5$  yr old) were uncommon. If large males play a role in timing and synchrony of reproduction, or degree of sociality, responses of females to males should be most pronounced under circumstances where large males are rare. Because of the scarcity of large males, group size and composition may be similarly affected by their presence, which

might lead to differences in mating behavior of bison.

Male mammals are known to influence reproductive behavior of females via pheromones in their urine (Izard & Vandenberg 1982; Menzies et al. 1992). Scent marking by dominant male ungulates, in addition to other functions, has been hypothesized to play a role in synchronizing and triggering estrus or ovulation in adult females (Gosling 1985; Bowyer & Kitchen 1987; Bakke & Figenschou 1990; Miquelle 1991; Bowyer et al. 1994; Oehler et al. 1995; Massei & Bowyer 1999; Whittle et al. 2000; Adams et al. 2001). American bison engage in scent-marking behaviors, including wallowing and rubbing of trees, which may serve those functions (Bowyer et al. 1998a). Moreover, large male bison scent mark more often than their smaller counterparts during rut (Bowyer et al. 1998a).

Female ungulates may adjust timing of estrus and dates of conception in relation to the age of available mates (Komers et al. 1999; Mysterud et al. 2002). Mating activities in populations composed of young male ungulates lead to more females being bred during their second estrus (Noyes et al. 1996, 2002). The absence of large male bison resulted in more sexual and aggressive interactions by younger males and excessive harassment of females (Komers et al. 1994). Such harassment of females by young males may have negative consequences for reproductive females, as reported in other ruminants (Singer & Zeigenfuss 2002). Consequently, there are potential benefits to females that mate with large males.

Northern populations of bison typically rut in August, although reproductive activity may extend over longer periods; the estrous cycle of females is approx. 23 d (Kirkpatrick et al. 1991). Length of gestation in American bison ranges from approx. 262 to 293 d (Berger & Cunningham 1994; Towne 1999). Some ungulates, including bison, are thought to adjust gestation length (Rachlow & Bowyer 1991; Berger 1992; Schwartz & Hundertmark 1993), but timing and synchrony of copulation and insemination likely influence birth dates. Bison exhibit considerable variation in dates of birth among populations (Rutberg 1984; Shaw & Carter 1989; Green & Rothstein 1993a; Berger & Cain 1999; Gogan et al. 2005). There are, however, strong environmental constraints on timing and synchrony of births among northern ungulates (Bowyer 1991; Rachlow & Bowyer 1991; Berger & Cunningham 1994; Hass 1997; Bowyer et al. 1998b; Rubin et al. 2000).

Reproductive activities of bison become more synchronous with increasing north latitude (Berger & Cunningham 1994). This pattern is thought to result from inhospitable conditions at the start of spring selecting against early births. Moreover, a limited time for late-born individuals to acquire resources necessary to survive winter during a short growing season selects against late births (Rachlow and Bowyer 1994). Neonates born late in the birthing season tend to be smaller and suffer higher mortality than those born earlier (Keech et al. 2000; Côté & Festa-Bianchet 2001). There are persistent influences of birth date on size, dominance, and reproductive success in bison (Green & Rothstein 1993b). Consequently, timing of mating by individuals likely is under strong selection; when a female conceives clearly is a critical component in the life-history tactics of these large herbivores.

We postulated that if large males were triggering estrus or ovulation, the timing of scent-marking behaviors by large males would slightly precede or be coincident with copulations. Scent marking should occur principally in a male-female context and take place frequently in groups with only one large male, where fights between large males are not possible. Moreover, we hypothesized that groups with large males would be larger than those with smaller males if large males are a critical component of mating activities. Likewise, we predicted that the presence of a large male in a group would lead to more copulations than in groups containing younger males. We further postulated that synchrony of reproductive activities in bison would be greater in Alaska than reported for populations inhabiting more southerly latitudes. We recognize that other hypotheses, which are not mutually exclusive, may explain variation in group size of bison (*sensu* Alexander 1974) and thereby affect mating activities. Accordingly, we also tested for effects of vegetation type, weather conditions, and predation risk on group size of bison. We had a unique opportunity to examine potential effects of predation risk on sociality of bison because of the large mammalian carnivores that co-occurred with this bison herd.

## Materials and Methods

### Study Area

We conducted research on American bison on the Delta Junction Bison Range (63°50'N, 145°10'W) in interior Alaska, approx. 260 km southeast of Fairbanks, Alaska, USA. The Delta Bison Range is

6500 ha, and portions of the range are managed intensively by the Alaska Department of Fish and Game to lure bison away from nearby agricultural crops composed predominantly of barley and oats. The study area is relatively flat and occurs at an elevation of approx. 310 m.

The climate is characteristic of interior Alaska. Mean annual temperature is  $-3.5^{\circ}\text{C}$  and the area receives 25–30 cm of annual precipitation. Summers are short but hot, with temperature sometimes reaching  $30^{\circ}\text{C}$ . Winters are harsh with snowfall typically occurring in late August and often persisting for 8 mo; occasionally temperature fall below  $-40^{\circ}\text{C}$ . High winds may occur in any month.

In 1996, we observed bison on the Panoramic (approx. 990 ha) and Gerstle (approx. 500 ha) fields; observations were restricted to the Panoramic Fields in 1997. Many of the fields on the Delta Junction Bison Range were plowed, planted with oats and blue grass, fertilized, burned, and some areas, mowed, to make the fields attractive to bison. These management activities were more intense on the Panoramic than Gerstle fields. Areas surrounding the fields were characterized by an overstory of black spruce (*Picea mariana*) and aspen (*Populus tremuloides*) with an understory of willows (*Salix* spp.). We observed gray wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) on the study area; both are predators of bison, especially on young animals (McHugh 1972; Carbyn & Trottier 1987; Carbyn et al. 1993; Smith et al. 2000; Wyman 2002).

Bison did not use the Delta Junction Bison Range year-round, but groups of bison began migrating into the area during mid- to late July (Bowyer et al. 1998a). Most dimorphic ruminants (Bowyer 2004), including bison (Berger & Cunningham 1994; Post et al. 2001; Mooring et al. 2005), sexually segregate for much of the year, and form mixed-sex groups predominantly during rut (Schuler et al. 2006). The peak of rut for bison on our study area occurred in August (Bowyer et al. 1998a); nevertheless, births may be spread over >1 mo in some populations of bison (Berger & Cunningham 1994; Berger & Cain 1999).

The Delta Junction bison herd was established with a translocation of 23 plains bison (*B. b. bison*) from the National Bison Range in Moise, Montana, USA, in 1928. Wood bison (*Bison bison athabasca*), however, occurred naturally in Alaska into recent times (Guthrie 1990). The Delta Junction bison herd numbered approx. 450 animals during our study, and both sexes were harvested annually under a permit system administered by the Alaska Department of

Fish and Game. That harvest produced a skewed sex ratio in which large male bison were uncommon (Bowyer et al. 1998a). Hunting did not occur until after the periods when we observed bison.

### Sampling Methods

Sampling methods differed markedly between the study years. We sampled bison from Aug. 7 to Sep. 7, 1996 to obtain detailed records of scent marking and courtship behaviors, including copulations (Lott 1974), using an all-occurrences log (Altmann 1974). We distributed our sampling effort throughout the rut to obtain a representative sample, recording behaviors of bison for approx. 3 d/wk. Our procedure was to search until we encountered a large mixed-sex group of bison that could be observed at close distances (30–75 m) from a vehicle by a primary observer, who recorded data on a check sheet, and a secondary observer, who helped with timing of sampling intervals. Observations were made with 10× binoculars or the unaided eye of a particular group for as long as possible. We subdivided our observations into 15-min intervals to examine associations between the types of behaviors we recorded. We sometimes did not obtain a complete count of animals or categorize the entire group into sex and age classes; our observations were focused primarily on focal animals engaged in courtship, scent-marking, and aggressive behaviors. We also sampled the physical and spatial characteristics of wallows and rubbed trees, and described scent-marking behaviors by sex and age classes of bison (Bowyer et al. 1998a). All methods used in this study were in keeping with the procedures subsequently adopted by the American Society of Mammalogists for research on wild mammals (Animal Care and Use Committee 1998).

In 1997, we concentrated our efforts on obtaining detailed estimates of group size and composition throughout rut, and continued to sample mating activities. This change in sampling protocol was initiated because we recognized that mating activities were influenced by group dynamics, which were not sampled adequately in 1996. The change also was necessary to test hypotheses concerning the role of large vs. small males in mating success, which required detailed data on group composition. We observed bison, weather and logistics permitting, by driving a fixed route of 17.2 km each morning and evening from Aug. 8 to 27, 1997, with samples collected on approx. 4 d/wk. We sampled during mornings and evenings, because bison mate most

often during these periods (personal observations). The direction in which the route was traveled was changed with each sampling effort. Our route was located along the periphery of the Panoramic Field, which allowed a good view of bison in the open, manipulated areas. Samples in which some animals were obscured by vegetation or occasionally topographic relief were not included in analyses. All observations were made from a vehicle with the unaided eye, 10× binoculars, or a 20–60× spotting scope over distances of 30–300 m; data were recorded in the same manner as in 1996. Great care was taken not to disturb bison, and data collection was terminated if bison took flight, which occurred rarely (approx. one group per transect). We were not able to gather data on fleeing bison, which typically moved quickly into the nearby forest. Data were not included in analyses unless we obtained a complete count of bison composing a particular group, although sometimes we were unable to accurately assign all individuals to a sex and age class; such animals were categorized as ‘unknowns.’

We defined a group as  $\geq 1$  animal that was  $\leq 50$  m from one another and tended to move as a cohesive unit (Bowyer 1984; Bowyer et al. 2001). If any question arose as to whether an animal was a member of a particular group, we watched that individual until it either joined a group, or failed to do so, by the time we terminated observations. We watched bison groups carefully to be sure that we obtained a complete count, especially for groups near the forest edge. We included lone individuals in our analyses to encompass the complete range of sociality exhibited by this species (Bowyer et al. 2001; Monteith et al. 2007).

In both study years, we categorized bison by sex and age primarily on the basis of body size and horn characteristics (Fuller 1959, 1960; Berger & Cunningham 1994). Male bison could be assigned into five age classes based on these criteria (1 to  $\geq 5$  yr old). We divided male bison into 1–2, 3–4, and  $\geq 5$  yr olds because of similar behavior patterns within these age classes, and to increase sample sizes for some statistical analyses. A few males attain sexual maturity as yearlings, approx. 33% do so as 2 yr olds, and the remainder is sexually mature by 3 yr of age (Fuller 1961; Helbig et al. 2007). The large size and distinctive characteristics of horns for large males ( $\geq 5$  yr olds) made it possible to determine if a particular group contained those individuals in all but one instance. We acknowledge, however, that males may not reach full size until 8–11 yr old (Berger & Cunningham 1994), which makes our

analysis of the influence of large males on mating activities conservative.

Females were categorized as yearlings or adults ( $\geq 2$  yr old). Adult females were grouped into a single age class because they are capable of conception at 2 yr of age (Shaw & Carter 1989; Green & Rothstein 1991; Wolff 1998), and because we could not discriminate age classes of adults during field observations. Young were animals of either sex  $< 1$  yr old.

For each group of bison encountered in 1997, we recorded, date, time, weather condition (clear, overcast, and rain or snow), location (Universal Transverse Mercator, UTM), vegetation type in which the group predominantly occurred (oats, unmowed bluegrass, and mowed bluegrass), the number of individuals and, where possible, their sex and age class. We visually estimated (nearest 5 m) the distance from the nearest side of the group to the edge of the forest as an index to predation risk (Bowyer et al. 2001), and the maximum distance across the group. We used the body length of bison (Berger & Cunningham 1994) and a map of the study area with UTM benchmarks to aid in this process. We divided the maximum distance across the group by group size to obtain a crude index of the clumping and cohesion of individuals within the group. For groups that we were able to observe clearly for  $\geq 15$  min, we noted the number of adult females with their tails held erect and with an enlarged vulva, which are reliable indicators of copulations occurring within the previous 6 h (Berger & Cunningham 1994; Wolff 1998). Observation times for groups of differing size were nearly equal.

The Alaska Department of Fish and Game previously captured and fitted 11 adult female bison with VHF radiocollars. In 1997, we surveyed each group we encountered, both visually and with radiotelemetry equipment, for the presence of animals equipped with radiocollars. These data allowed us to obtain a crude index of what proportion of the bison herd we sampled, and how often we were sampling the same individuals within or among days.

### Data Analyses

In 1997, we subdivided bison into three group-size categories based on natural breaks in quantiles of the distribution of group sizes: small ( $\leq 15$  animals), medium (16–39 animals), and large ( $\geq 40$  animals) groups. We created categories of group size for two reasons. First, categories are useful for data in which a large portion of samples falls within a small range, but may have valid extreme values (Johnston et al.

2001) that can have undue leverage on continuous models (Rousseeuw & Van Zomeren 1990). Second, categories may reveal non-linear relationships more easily than continuous data (Schmidt et al. 2007).

We categorized groups of bison according to the method of Hirth (1977), Bowyer (1984) and Bleich et al. (1997). Mixed-sex groups had at least one adult male ( $\geq 2$  yr old) and one adult female, but could contain other sex and age classes. Male groups contained only males  $> 1$  yr old and female groups were composed of adult females, and also could contain yearlings and young. Groups of male or female yearlings, or young included only those age classes.

In both years, we determined timing and synchrony of mating by bison, based on observations of copulations and the number of adult females with tails held erect. We used the method of Johnson et al. (2004), which allowed us to calculate a robust estimate of the mean (timing) and a corrected estimate of the SD of the distribution of events that are valid for determining synchrony. Moreover, this procedure allows for sampling with unequal time intervals (bin sizes), which heretofore has not been possible (Johnson et al. 2004). This technique also allowed a valid comparison between the years where sampling methods differed markedly, because sampling intervals and intensity need not be equal. We employed the same technique to examine the temporal distribution of scent marking by large males in 1996. Copulations could have a time lag of up to 6 h (e.g. those inferred from tails held erect), but scent-marking behaviors were observed directly over much shorter time intervals. Consequently, we pooled data on timing of these behaviors by day to avoid a temporal bias.

We analyzed data on sex and age composition of the bison herd with one-way analysis of variance (ANOVA) after completing an arc-sine square-root transformation on percentages (Zar 1999). A Bonferroni correction was applied to unplanned contrasts. We eliminated one group of bison from analyses of group composition because, although we obtained a count of bison, we categorized too few individuals to sex and age class.

Data on the observed and expected distributions of large males and adult females in small, medium, and large groups were examined with the multiway  $\chi^2$ -test (Zar 1999). We used the G-test, following Yates correction, for examining differences in the number of tails held erect (copulations) in groups with and without large males. We used linear regression to test for relationships between distance from the edge of the forest with group size and cohesion.

We employed one-way ANOVA to compare group sizes among habitat types. Differences in size of groups with and without large males and timing of life-history events were examined with t-tests (Zar 1999). An  $\alpha = 0.02$  was adopted for these statistical tests, all of which were two-tailed. We arbitrarily reduced alpha from 0.05 to 0.02 to help correct for effects of inflating sample size by making repeated observations on the same bison, most of which could not be identified as individuals.

We used the two-sample Z-test to compare differences in the proportion of scent marking that co-occurred with sexual or other scent marking (e.g. both sexes scent-marked together) with instances where no scent marking occurred but where we observed sexual behavior. For this test, the number of 15-min intervals in which we made observations was the sampling unit. This test is especially appropriate for this comparison because it allows sampling with replacement (Schork & Remington 2000), and, as noted previously, some of our intervals contained observations on the same animals.

## Results

### Group Size and Composition

We made detailed behavioral observations on 20 mixed-sex groups of bison during 1996. We observed three of those groups that were  $> 100$  bison on the Panoramic Field, one of which included 197 individuals that composed  $> 43\%$  of the entire population. Bison groups were much larger in 1996 than in 1997, where the largest group included 86 individuals.

We observed 41 groups of bison composed of 1210 animals on the Panoramic Field in 1997. Mean ( $\pm$ SD) group size during rut was  $29.5 \pm 23.8$  (range = 1–86 animals; CV = 81%). Groups containing large males ( $\geq 5$  yr old) were significantly ( $t_{38} = 5.10$ ,  $p < 0.0001$ ) larger ( $44.3 \pm 24.50$ , range = 8–86,  $n = 20$ ) than groups without them ( $14.1 \pm 10.01$ , range = 1–34,  $n = 20$ ). Moreover, mean ( $\pm$ SE) group size differed significantly ( $F_{2,37} = 18.16$ ,  $p < 0.0001$ ) among groups with zero ( $14.1 \pm 3.91$ ,  $n = 20$ ), one ( $40.1 \pm 4.24$ ,  $n = 17$ ), or two large males ( $68.0 \pm 10.10$ ,  $n = 3$ ). Overall, only 50% of bison groups contained large males. We observed a little variation in group composition during the observation periods.

We located 7 of 11 radiocollared females in our study area using radiotelemetry and direct observations. These seven bison were observed a mean of 3.9 times each during 1997, with a maximum of

seven collared females present on any day. We detected some collared bison on all but 2 d of sampling. Only once, however, we sampled the same collared individual in both morning and evening surveys. We observed a mean ( $\pm$ SD) of  $134.5 \pm 46.23$  animals each day, approx. 30% of the estimated 450 bison in the Delta Junction herd.

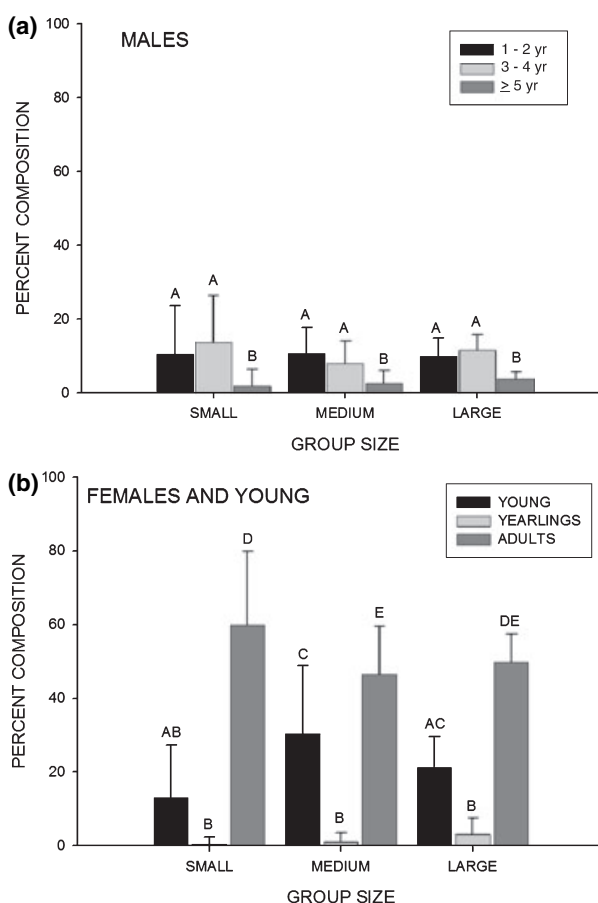
In 1997, 40 groups of bison occurred in mixed-sex (90%) or female groups (10%); we observed no male-only groups, or groups of young or yearling females without adult females. The overall sex ratio of large males to smaller males (1–4 yr old) to adult females was 6:64:100, respectively. Indeed, groups were composed predominantly of adult females; young were distributed across all categories of group size, with proportionately fewer young in small groups (Fig. 1). Males were a small percentage of all groups; large males ( $\geq 5$  yr old) were particularly uncommon in any size of bison group, but occurred across all group sizes (Fig. 1).

Large male (partial  $\chi^2_2 = 12.03$ ,  $p < 0.01$ ) and adult female (partial  $\chi^2_2 = 116.14$ ,  $p < 0.0001$ ) bison occurred disproportionately in large groups and less often in small ones compared with their expected distributions (Fig. 2). This pattern, however, was more pronounced for large males than for females ( $\chi^2_3 = 128.18$ ,  $p < 0.0001$ ). These outcomes on group composition ostensibly occurred because large males composed such a small proportion of the total herd (Fig. 1), and there were many groups without large males.

#### Effects of Vegetation Type, Weather, and Predation Risk

Mean ( $\pm$ SE) group size of bison did not vary ( $F_{2,36} = 1.24$ ,  $p = 0.30$ ) with the type of manipulated vegetation they occupied: oats ( $34.6 \pm 5.11$ ,  $n = 19$ ); un-mowed bluegrass ( $23.8 \pm 5.96$ ,  $n = 14$ ); and mowed bluegrass ( $22.5 \pm 9.10$ ,  $n = 6$ ) during 1997. Likewise, weather conditions: clear ( $29.3 \pm 8.85$ ,  $n = 7$ ); overcast ( $31.8 \pm 5.52$ ,  $n = 18$ ); and rain or snow ( $28.8 \pm 11.71$ ,  $n = 4$ ) had no effect on group sizes of bison in 1997 ( $F_{2,26} = 0.05$ ,  $p = 0.96$ ).

Overall, 41 groups of bison occurred a mean ( $\pm$ SD) distance of  $65.0 \pm 62.05$  m (range = 1–220 m) from the forest edge in 1997. Distance from the forest to the nearest edge of a bison group was positively related to group size (Fig. 3). Mean ( $\pm$ SD) distance across the group ( $n = 35$  groups) was  $79.1 \pm 66.87$  m (range = 3–300 m) in 1997. The composite variable representing clumping (distance across the herd/group size:  $3.3 \pm 1.58$ , range = 1.3–



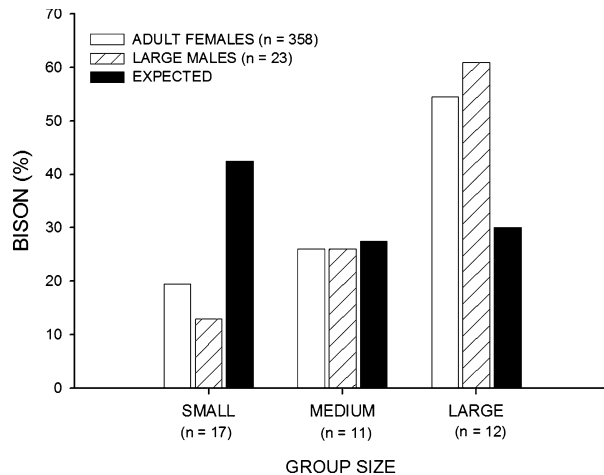
**Fig. 1:** Mean ( $\pm$ SE) sex and age composition of 40 groups of American bison subdivided in to small (<15 animals), medium (16–39 animals), and large (>40 animals) groups for (a) males and (b) females and young, observed on the Delta Junction Bison Range in interior Alaska, USA, during Aug. 1997. Composition of sex and age classes sum to 100% across all group sizes. Differences in age composition were tested with anova (females and young,  $p < 0.0001$ ; males,  $p = 0.003$ ). Different capital letters above error bars indicate significant differences ( $p \leq 0.02$ ) following pairwise comparisons and a Bonferroni correction.

7.5) was inversely, but not significantly, related to distance to the forest edge ( $r^2 = 0.05$ ,  $p = 0.211$ ).

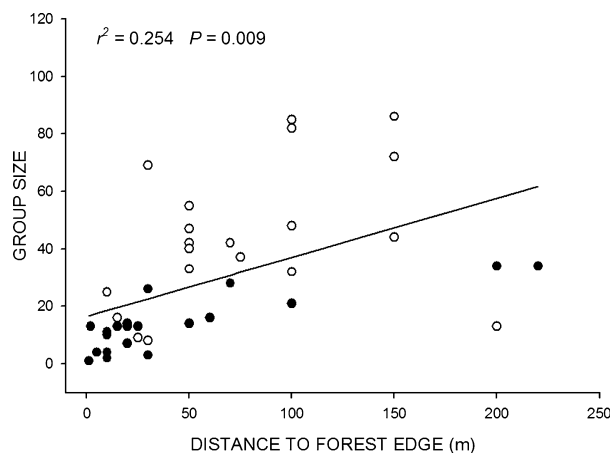
#### Timing and Synchrony of Mating

In 1996, we directly observed 26 copulations, followed by female bison immediately holding their tails erect, and inferred copulation from a female with an erect tail. In 31 instances of mating behavior by adult females in 1997, we directly observed nine copulations; the remainder was inferred from females with their tails erect.

Bison exhibited extreme synchrony in mating, but timing was nearly identical between years.



**Fig. 2:** Percent occurrence of large male ( $\geq 5$  yr old) and adult female ( $\geq 2$  yr old) American bison in small ( $< 15$  animals), medium (16–39 animals), and large ( $> 40$  animals) groups observed on the Delta Junction Bison Range in interior Alaska, USA, during Aug. 1997. Expected values were obtained by allocating the overall mean number of large males or adult females in all groups to bison in small, medium, or large groups.



**Fig. 3:** Linear relationship ( $\hat{Y} = 16.95 + 0.19x$ ) between group size and distance to the forest edge for all groups of American bison with large males (open circles) and without large males (closed circles) observed on the Delta Junction Bison Range in interior Alaska, USA, during Aug. 1997.

Mean ( $\pm$ SD) date of mating in bison was Aug.  $18 \pm 5.1$  d ( $n = 27$ ) in 1996, and Aug.  $20 \pm 6.2$  d ( $n = 31$ ) in 1997. Timing of mating was not significantly different between years ( $t_{57} = 1.33$ ,  $p = 0.19$ ). Robust, unbiased estimates of the SD indicated that 67% of mating occurred in approx. 10 d, and 95% in approx. 20 d in 1996. In 1997, 67% of mating occurred in approx. 12 d, and 95% in approx. 24 d. Variation in timing of mating within years differed

little (1996 CV = 22%; 1997 CV = 27%) further indicating strong synchrony in this behavior. Overall, mating activity was highly concentrated in August.

### Effects of Large Males on Mating

The presence of a large male ( $\geq 5$  yr old) bison had a profound effect on mating behavior of adult females. Females were more likely to mate when a large male was present compared with groups where only smaller males (1–4 yr old) occurred. We observed 26 females with tails held erect in 18 groups containing large males, but only on five occasions were tails erect in 14 groups with smaller males ( $G_1 = 164.44$ ,  $p < 0.0001$ ).

We observed 45 bouts of scent marking by large male bison in 1996 (40 wallows and five tree rubs). We evaluated the presence or absence of scent marking in sexual and aggressive behaviors in bison by examining those behaviors in 15-minute intervals ( $n = 90$ ). All rubbing of trees by large males was accompanied by wallowing. We documented the co-occurrence of wallowing ( $n = 23$  intervals), including simultaneous wallowing by large males and adult females, and sexual behaviors by large males (tending, licking of females, flehmen, and copulation). Intervals involving wallowing were compared with instances during which no wallowing occurred ( $n = 49$ ) but sexual behaviors were observed. The proportion of wallowing by large males followed by sexual activities (0.74) was significantly greater ( $Z = 2.68$ ,  $p = 0.007$ ) than for the proportion of intervals in which no wallowing was observed but sexual behavior occurred (0.43). We observed only three fights among large males; two were accompanied by wallowing and one was not; sample sizes were too small for statistical analysis, but these were the only instances where  $> 1$  large male was in the same group. Most scent marking occurred in a male–female context.

Mean timing (Aug.  $20 \pm 9.7$  d, CV = 42%) of scent marking by large males during 1996 was not different from the chronology of mating ( $t_{70} = 0.99$ ,  $p = 0.33$ ). Scent marking, however, was somewhat less synchronous than copulations (CVs = 42% vs. 22%, respectively).

### Discussion

Our observations likely reflect the overall behavior of bison we studied because of our systematic sampling scheme. We also employed an analytical

technique (e.g. Johnson et al. 2004), which allowed comparisons of behaviors between years with different sampling intervals. Other evidence that our samples are likely representative of the Delta Junction herd includes the large groups of bison we observed in 1996, which in one instance constituted >40% of the herd. We also consistently located the most telemetered females and observed approx. 30% of the herd in daily surveys in 1997. Consequently, we believe our data are representative of the behaviors for that herd.

One problem we encountered was not being able to consistently recognize individual bison. We compensated for this shortcoming in several ways. First, where possible, we used statistics that allowed sampling with replacement for tests involving differences in proportions (Schork & Remington 2000). Second, although sample size was small, telemetered females were seldom sampled twice in the same day, indicating that groups likely changed composition between sampling transects, and many of our analyses used the group as the sampling unit. Finally, we reduced alpha from 0.05 to 0.02 to compensate for inflating sample size by resampling the same individuals on some occasions.

Data on timing of mating revealed a high degree of synchrony, with little between-year variation. Berger & Cunningham (1994) likewise observed little among-year variation in timing of births for bison, but Green & Rothstein (1993a) noted more interannual variability. Our data on mating of bison in Alaska indicate somewhat greater synchrony than Berger & Cunningham (1994) reported, and considerable more synchrony than Green & Rothstein (1993a) described for parturition, an outcome consistent with the hypothesis of greater synchrony in reproductive activities with increasing north latitude (Berger & Cunningham 1994). Mating by bison in Alaska was highly clumped within August, with very small standard deviations (synchrony) in both years. Such synchrony in reproductive activities is typical for ungulates living in the far north (Eastland et al. 1989; Rachlow & Bowyer 1991; Bowyer et al. 1998b; Barton et al. 2001).

Gestation lengths in bison are variable (Berger 1992). Factors such as nutritional status and the presence of disease may affect timing of births (Berger & Cain 1999; Keech et al. 2000) – timing and synchrony of mating clearly have a strong influence on when neonates are born. Consequently, mating and its effects on timing of parturition are critical components in the fitness of individual northern ungulates (Green & Rothstein 1993b; Keech et al.

2000; Côté & Festa-Bianchet 2001). Bison births may occur over >1 mo (Green & Rothstein 1993a; Berger & Cunningham 1994). Nonetheless, data on survivorship of these young are sparse, especially for populations where predation still is an important component in mortality of young bison. The timing of mating we observed in August likely indicates an adaptive advantage to such synchronous mating.

The occurrence of large groups of bison in the Delta Junction herd in 1996 compared with 1997 did not significantly alter timing of mating. This outcome indicates that more than just social facilitation (*sensu* Asher et al. 1996) associated with large groups affected these reproductive activities, at least for the sizes of groups that we observed. We hypothesize that the presence of large males was an important factor in timing of mating behavior. Indeed, females in groups with large males were far more likely to copulate than those in groups with smaller males. This outcome indicates that females prefer to mate with large males, even when these individuals are rare.

Large males occurred disproportionately in large compared with small groups (Fig. 2), and composed only 50% of all groups we observed in 1997. These outcomes are in keeping with a pattern of large males seeking female groups rather than vice versa. We would have expected females to have concentrated around rare, large males if they were primarily responsible for formation of mixed-sex groups – there were many groups of female bison without large males. Large males occurring across all sizes of groups (Fig. 1) also may indicate that these males were evaluating the reproductive potential of some females and directing their courtship activities accordingly (Berger 1989). These hypotheses, however, require additional testing with more concentrated observations on group formation and movements of sexes among groups. We could not evaluate changes in group formation because group composition of bison changed little during our observation periods.

Wallowing and rubbing of trees by American bison may have additional functions, but these behaviors clearly are used for scent marking by large males during rut (Bowyer et al. 1998a). Scent urination is common among male ungulates (Bowyer & Kitchen 1987; Miquelle 1991), and the association of urinating and wallowing by large male bison links these behaviors with the pattern observed in other species (Bowyer et al. 1998a). Rubbing of trees and shrubs likewise is widely recognized as a form of scent marking (Bowyer & Kitchen 1987; Benner &



Bowyer 1988; Bowyer et al. 1994; Oehler et al. 1995; Massei & Bowyer 1999; and many others). Had wallowing functioned predominantly for purposes other than scent marking, we would not have expected large male bison to have engaged in this behavior more often than other sex and age classes (Bowyer et al. 1998a). Likewise, we would not have predicted such strong concordance in timing of scent marking and mating.

Scent marking by large males was less synchronous than mating. Moreover, scent marking was timed such that it is unlikely that this behavior was involved in priming estrus (at least for the first estrous cycle), which is approx. 23 d in bison (Kirkpatrick et al. 1991). The near-identical timing of scent marking and mating by large males, however, is consistent with the hypothesis of males triggering ovulation, especially because scent marking was linked more strongly with sexual behavior than male-male aggression, and was preformed more often by large than smaller males (Bowyer et al. 1998a).

Scent marking occurred in many groups that contained only one large male bison, where there was no opportunity for scent marking to be involved in aggression between large males. Other behaviors by large males might influence timing of reproduction. Nevertheless, this possibility would not explain the strong relationship we observed between scent marking and sexual behavior in bison, or the well-established role of male pheromones influencing reproductive behavior in female mammals (Izard & Vandenberg 1982; Rasmussen 1988; Menzies et al. 1992; Rasmussen & Perin 1999). We believe our observations offer support for scent marking by large males influencing reproductive activity of females, but a critical test of this hypothesis likely would require experiments on the physiology and behavior of captive bison.

Sociality often is promoted by an intensified risk of predation (Alexander 1974). Plains bison historically occurred mostly in open habitats (McHugh 1972), although some bison also inhabited forested mountains (Fryxell 1928). Our data indicated that distance to the forest edge was related to group size and that cover may allow bison to elude predators in forested environments. Bison that we disturbed uniformly fled to the forest. Van Vuren (1983) also reported that group size in bison increased as they occupied more open habitats. Nevertheless, smaller groups of bison may have been present in forested areas where we could not observe them. Indeed, Melton et al. (1989) reported comparatively small

group sizes for bison, ostensibly because they used the forest for feeding during autumn.

In some instances, the forest edge also may offer cover for stalking wolves (Kunkel & Pletscher 2001). Moreover, cervids may perceive forest edges as riskier than open areas (Altendorf et al. 2001). Nonetheless, cervids often are confronted with ambush predators such as mountain lions (*Puma concolor*), near forest edges, but coursing predators, such as wolves and coyotes (*Canis latrans*) still can promote group formation at increasing distances from concealment cover (Dale et al. 1994; Molvar & Bowyer 1994; Bowyer et al. 2001; Pierce et al. 2004). Our results (Fig. 3) are consistent with an increase in group size with increasing distance from escape or concealment cover as an adaptation to reduce predation, a pattern common to many social ungulates (Hirth 1977; Berger 1978, 1991; Underwood 1982; LaGory 1986; Molvar & Bowyer 1994; Rachlow & Bowyer 1998; Bowyer et al. 2001).

Hunting also may have affected grouping patterns of bison. Nevertheless, sport hunting and predation can have quite different effects on social behavior and demographics of ungulate populations (Berger 2005). We foresee little advantage to bison forming large groups in open areas in response to human hunting, which involves modern high-powered rifles and ammunition. Although factors such as predation risk clearly influenced group size in bison, benefits from the presence of large males also played a strong role in mating activities. The presence of large males may be critical to the dynamics of some ungulate populations (Myserud et al. 2002; Rankin & Kokko 2007). We hypothesize that large groups of bison offer a reduced risk from predation and an added benefit related to timing of mating for individual females that occur with large males.

Several aspects of our study are unique and provide general insights into the behavior of bison. Because large males were exceptionally scarce, we were able to clearly document that females preferred to mate with large compared with smaller males, although males likely sought out groups of females rather than vice versa. Moreover, large males played an important role to the degree of sociality exhibited by bison – groups with large males were larger than those without them. Scent-marking behavior by large males was more frequent than for smaller males (Bowyer et al. 1998a), and occurred primarily in a male-female context. Timing of scent marking was concordant with highly synchronous mating activities by bison, which supports the hypothesis

that scent marking triggers ovulation in females. Research on captive animals, however, may be necessary to fully test this hypothesis. Nonetheless, quantitative and unbiased data on timing of life-history events are rare, and our method provides an illustration of how to compare timing and synchrony of social behaviors that play a critical role in the reproductive success of these unique large mammals. In addition, behavioral observations of bison in environments with a complete complement of natural predators are uncommon. In this predator-rich ecosystem, we demonstrated that group size of bison was directly related to distance to the forest edge, ostensibly a response to predation risk. This relationship likely plays an important role in the evolution of sociality for this gregarious large mammal.

### Acknowledgements

We thank S. DuBois of the Alaska Department of Fish and Game for his assistance with our research. A. Hoymork assisted with field work, and M. W. Oehler, Sr helped with data management. J. G. Kie provided a helpful review of our paper. This research was supported in part by the Institute of Arctic Biology at the University of Alaska Fairbanks, the Department of Biological Sciences at Idaho State University, and the School of Veterinary Science at the Autonomous University of Barcelona in Spain. This is Professional Paper 060 from the Eastern Sierra Center for Applied Population Ecology.

### Literature Cited

- Adams, C. A., Bowyer, R. T., Rowell, J. E., Hauer, W. E. & Jenks, J. A. 2001: Scent marking by male caribou: an experimental test of rubbing behavior. *Rangifer* **21**, 21–27.
- Alexander, R. D. 1974: The evolution of social behavior. *Ann. Rev. Ecol. Syst.* **5**, 325–383.
- Altendorf, K. B., Laundré, J. W., López González, C. A. & Brown, J. S. 2001: Assessing effects of predation risk on foraging behavior of mule deer. *J. Mammal.* **82**, 430–439.
- Altmann, J. 1974: Observational study of behaviour: sampling methods. *Behaviour* **49**, 227–267.
- Animal Care and Use Committee. 1998: Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *J. Mammal.* **79**, 16–31.
- Asher, G. W., Fisher, M. W. & Fennessy, P. F. 1996: Environmental constraints on reproductive performance of farmed deer. *Anim. Reprod. Sci.* **42**, 35–44.
- Bakke, J. M. & Figenschou, E. 1990: Volatile compounds for the red deer (*Cervus elaphus*). Substances secreted via the urine. *Comp. Biochem. Physiol.* **97A**, 427–431.
- Barton, N. L., Bowyer, R. T. & Jenkins, K. J. 2001: Habitat use by female caribou: tradeoffs associated with parturition. *J. Wildl. Manage.* **65**, 77–92.
- Benner, J. M. & Bowyer, R. T. 1988: Selection of trees for rubs by white-tailed deer in Maine. *J. Mammal.* **69**, 624–627.
- Berger, J. 1978: Group size, foraging, and antipredator ploys: analysis of bighorn sheep decisions. *Behav. Ecol. Sociobiol.* **4**, 91–99.
- Berger, J. 1989: Female reproductive potential and its apparent evaluation by male mammals. *J. Mammal.* **70**, 347–358.
- Berger, J. 1991: Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Anim. Behav.* **41**, 61–77.
- Berger, J. 1992: Facilitation of reproductive synchrony by gestation adjustment: a new hypothesis. *Ecology* **73**, 323–329.
- Berger, J. 2005: Hunting by carnivores and humans: does functional redundancy occur and does it matter. In: *Large Carnivores and the Conservation of Biodiversity* (Ray, J. C., Redford, K. H., Steneck, R. S. & Berger, J., eds). Island Press, Covelo, CA, pp. 315–341.
- Berger, J. & Cain, S. L. 1999: Reproductive synchrony in brucellosis-exposed bison in the southern greater Yellowstone ecosystem and in noninfected populations. *Conservation Biology* **13**, 357–366.
- Berger, J. & Cunningham, C. 1994: *Bison: Mating and Conservation in Small Populations*. Columbia Univ. Press, New York, NY.
- Berger, J. & Peacock, D. M. 1988: Variability in size–weight relationships of *Bison bison*. *J. Mammal.* **69**, 618–624.
- Bleich, V. C., Bowyer, R. T. & Wehausen, J. D. 1997: Sexual segregation in mountain sheep: resources or predation? *Wildl. Monogr.* **134**, 1–50.
- Bowyer, R. T. 1981: Activity, movement, and distribution of Roosevelt elk during rut. *J. Mammal.* **62**, 574–582.
- Bowyer, R. T. 1984: Sexual segregation in southern mule deer. *J. Mammal.* **65**, 410–417.
- Bowyer, R. T. 1991: Timing of parturition and lactation in southern mule deer. *J. Mammal.* **72**, 138–145.
- Bowyer, R. T. 2004: Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. *J. Mammal.* **85**, 1039–1052.
- Bowyer, R. T. & Kitchen, D. W. 1987: Significance of scent-marking by Roosevelt elk. *J. Mammal.* **68**, 418–423.

- Bowyer, R. T., Van Ballenberghe, V. & Rock, K. R. 1994: Scent marking by Alaskan moose: characteristics and spatial distribution of rubbed trees. *Can. J. Zool.* **72**, 2186–2192.
- Bowyer, R. T., Manteca, X. & Hoymork, A. 1998a: Scent marking in American bison: morphological and spatial characteristics of wallows and rubbed trees. In: *International Symposium on Bison Ecology and Management in North America* (Irby, L. R. & Knight, J. E., eds). Montana State Univ., Bozeman, MT, pp. 81–91.
- Bowyer, R. T., Van Ballenberghe, V. & Kie, J. G. 1998b: Timing and synchrony of parturition in Alaskan moose long term versus proximal effects of climate. *J. Mammal.* **79**, 332–344.
- Bowyer, R. T., McCullough, D. R. & Belovsky, G. E. 2001: Causes and consequences of sociality in mule deer. *Alces* **37**, 371–402.
- Carbyn, L. & Trottier, T. 1987: Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. *Can. J. Zool.* **65**, 2072–2078.
- Carbyn, L. N., Oosenbrug, S. M. & Anions, D. W. 1993: Wolves, Bison and the Dynamics Related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park. Canadian Circumpolar Institute, Univ. Alberta. Circumpolar Research Series No. 4. Canadian Circumpolar Institute, Alberta, pp. 1–270.
- Côté, S. D. & Festa-Bianchet, M. 2001: Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* **127**, 230–238.
- Dale, B. W., Adams, L. G. & Bowyer, R. T. 1994: Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *J. Anim. Ecol.* **63**, 644–652.
- Eastland, W. G., Bowyer, R. T. & Fancy, S. G. 1989: Effects of snow cover on selection of calving sites by caribou. *J. Mammal.* **70**, 824–828.
- Fryxell, F. M. 1928: The former range of bison in the Rocky Mountains. *J. Mammal.* **9**, 129–139.
- Fuller, W. A. 1959: The horns and teeth as indicators of age in bison. *J. Wildl. Manage.* **23**, 342–344.
- Fuller, W. A. 1960: Behavior and social organization of the wild bison of Wood Buffalo National Park. *Can. Wildl. Serv. Wildl. Manage. Bull.* **1**, 1–52.
- Fuller, W. A. 1961: The ecology and management of the American bison. *Terre et la Vie*. **2**, 286–304.
- Gogan, P. J. P., Podrusny, K. M., Olexa, E. M., Pac, H. I. & Frey, K. L. 2005: Yellowstone bison fetal development and phenology of parturition. *J. Wildl. Manage.* **69**, 1716–1730.
- Gosling, L. M. 1985: The even toed ungulates: order Artiodactyla. Sources, behavioral context, and function of chemical signals. In: *Social Odours in Mammals* (Brown, R. E. & Macdonald, D. W., eds). Oxford Univ. Press, Oxford, pp. 560–618.
- Green, W. C. H. & Rothstein, A. 1991: Trade-offs between growth and reproduction in female bison. *Oecologia* **86**, 521–527.
- Green, W. C. H. & Rothstein, A. 1993a: Asynchronous parturition in bison: implications for the hider–follower dichotomy. *J. Mammal.* **74**, 920–925.
- Green, W. C. H. & Rothstein, A. 1993b: Persistent influences of birth date on dominance, growth and reproductive success in bison. *J. Zool. (Lond.)*. **230**, 177–186.
- Guthrie, R. D. 1990: *Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe*. Univ. of Chicago Press, Chicago, IL.
- Hass, C. C. 1997: Seasonality of births in bighorn sheep. *J. Mammal.* **78**, 1251–1260.
- Helbig, L., Woodbury, M. R., Haigh, J. C. & Barth, A. D. 2007: The onset of puberty in North American bison (*Bison bison*) bulls. *Anim. Reprod. Sci.* **97**, 12–24.
- Hirth, D. H. 1977: Social behavior of white-tailed deer in relation to habitat. *Wildl. Monogr.* **53**, 1–55.
- Izard, M. I. & Vandenberg, J. G. 1982: The effects of bull urine on puberty and calving date in crossbred beef heifers. *J. Anim. Sci.* **55**, 1160–1168.
- Johnson, D. S., Barry, R. P. & Bowyer, R. T. 2004: Estimating timing of life-history events with coarse data. *J. Mammal.* **85**, 932–939.
- Johnston, K., Ver Hoef, J. M., Krivoruchko, K. & Lucas, N. 2001: *Using ArcGIS Geostatistical Analyst*. ESRI Press, Redlands, CA.
- Keech, M. A., Bowyer, R. T., Ver Hoef, J. M., Boertje, R. D., Dale, B. W. & Stephenson, T. R. 2000: Life-history consequences of maternal condition in Alaskan moose. *J. Wildl. Manage.* **64**, 450–462.
- Kirkpatrick, J. F., Kincy, V., Bancroft, K., Shideler, S. E. & Lasley, B. L. 1991: Estrous cycle of the North American bison (*Bison bison*) characterized by urinary pregnanediol 3-glucuronide. *J. Rep. Fert.* **93**, 541–547.
- Komers, P. E., Messier, F. & Gates, C. C. 1994: Plasticity of reproductive-behavior in wood bison bulls: when subadults are given a chance. *Ethol. Ecol. Evol.* **6**, 313–330.
- Komers, P. E., Birgersson, B. & Ekvall, K. 1999: Timing of estrus in fallow deer is adjusted to the age of available mates. *Am. Nat.* **153**, 431–436.
- Kunkel, K. & Pletscher, D. H. 2001: Winter hunting patterns of wolves in and near Glacier National Park, Montana. *J. Wildl. Manage.* **65**, 520–530.
- LaGory, K. E. 1986: Habitat, group size, and the behaviour of white-tailed deer. *Behaviour* **98**, 168–179.
- Lott, D. F. 1974: Sexual and aggressive behavior in bison. In: *The Behaviour of Ungulates and Its Relation to Management* (Geist, V. & Walther, F., eds). New Series 24, IUCN, Morges, Switzerland, pp. 382–394.

- Lott, D. F. 1979: Dominance relations and breeding rate in mature male American bison. *Z. Tierpsychol.* **49**, 418–432.
- Lott, D. F. 1981: Sexual behavior and intersexual strategies in American bison. *Z. Tierpsychol.* **56**, 97–114.
- Lott, D. F. 1985: Individual variation in fecundity in an American bison population. *Mammalia* **49**, 300–302.
- Maher, C. R. & Byers, J. A. 1987: Age-related changes in reproductive effort of male bison. *Behav. Ecol. Sociobiol.* **21**, 91–96.
- Massei, G. & Bowyer, R. T. 1999: Scent marking in fallow deer: effects of lekking behavior on rubbing and wallowing. *J. Mammal.* **80**, 633–638.
- McHugh, T. 1972: *The Time of the Buffalo*. Alfred A. Knopf, New York, NY.
- Melton, D. A., Larter, N. C., Gates, C. C. & Virgl, J. A. 1989: The influence of rut and environmental factors of the behaviour of wood bison. *Acta Theriol.* **34**, 179–193.
- Menzies, R. A., Heth, G., Ikan, R., Weinstein, V. & Nevo, E. 1992: Sexual pheromones in lipids and other fractions from urine of the male mole rat (*Spalax ehrenbergi*). *Physiol. Behav.* **52**, 741–747.
- Miquelle, D. G. 1991: Are moose mice? The function of scent urination in moose. *Am. Nat.* **138**, 112–119.
- Molvar, E. M. & Bowyer, R. T. 1994: Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *J. Mammal.* **75**, 621–630.
- Monteith, K. L., Sexton, C. L., Jenks, J. A. & Bowyer, R. T. 2007: Evaluation of techniques for categorizing sexual segregation. *J. Wildl. Manage.* **71**, 1712–1716.
- Mooring, M. S. et al. 2005: Sexual segregation in bison: a test of multiple hypotheses. *Behaviour* **142**, 897–927.
- Mysterud, A., Coulson, T. & Stenseth, N. C. 2002: The role of males in the dynamics of ungulate populations. *J. Anim. Ecol.* **71**, 907–915.
- Mysterud, A., Langvatn, R. & Stenseth, N. C. 2004: Patterns of reproductive effort in male ungulates. *J. Zool. (Lond.)* **264**, 209–215.
- Noyes, J. H., Johnson, B. K., Bryant, L. D., Findholt, S. L. & Thomas, J. W. 1996: Effects of bull age on conception dates and pregnancy rates in cow elk. *J. Wildl. Manage.* **60**, 508–517.
- Noyes, J. H., Johnson, B. K., Dick, B. L. & Kie, J. G. 2002: Effects of male age and female nutritional condition on elk reproduction. *J. Wildl. Manage.* **66**, 1301–1307.
- Oehler, M. W. Sr., Jenks, J. A. & Bowyer, R. T. 1995: Antler rubs by white-tailed deer: the importance of trees in a prairie environment. *Can. J. Zool.* **73**, 1383–1386.
- Pierce, B. M., Bowyer, R. T. & Bleich, V. C. 2004: Habitat selection by mule deer: forage benefits or risk of predation? *J. Wildl. Manage.* **68**, 533–541.
- Post, D. M., Armbrust, T. S., Horne, E. A. & Goheen, J. R. 2001: Sexual segregation results in difference in content and quality of bison (*Bos bison*) diets. *J. Mammal.* **82**, 407–413.
- Rachlow, J. L. & Bowyer, R. T. 1991: Interannual variation in timing and synchrony of parturition in Dall's sheep. *J. Mammal.* **72**, 487.
- Rachlow, J. L. & Bowyer, R. T. 1994: Variability in maternal behavior of Dall's sheep: environmental tracking or adaptive strategy? *J. Mammal.* **75**, 328–337.
- Rachlow, J. L. & Bowyer, R. T. 1998: Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. *J. Zool. (Lond.)* **245**, 457–465.
- Rankin, D. J. & Kokko, H. 2007: Do males matter? The role of males in population dynamics. *Oikos* **116**, 335–348.
- Rasmussen, L. E. L. 1988: Chemosensory responses in two species of elephants to constituents of temporal gland secretion and musth urine. *J. Chem. Ecol.* **14**, 1687–1711.
- Rasmussen, L. E. L. & Perin, T. E. 1999: Physioloigcal correlates of musth: lipid metabolites and chemical composition of exudates. *Physiol. Behav.* **67**, 539–549.
- Roden, C., Hilde, V., Guy, M. & Linda, V. E. 2003: Reproduction of bison bulls (*Bison bison bison*) in semi-natural conditions. *Anim. Reprod. Sci.* **79**, 33–43.
- Rousseeuw, P. J. & Van Zomeren, B. C. 1990: Unmasking multivariate outliers and leverage points. *J. Am. Stat. Assoc.* **85**, 633–639.
- Rubin, E. S., Boyce, W. M. & Bleich, V. C. 2000: Reproductive strategies of desert bighorn sheep. *J. Mammal.* **81**, 769–786.
- Rutberg, A. T. 1984: Birth synchrony in American bison: response to predation or season? *J. Mammal.* **65**, 418–423.
- Schmidt, J. I., Ver Hoef, J. M. & Bowyer, R. T. 2007: Antler size of Alaskan moose: effects of population density, harvest intensity, and use of guides. *Wildl. Biol.* **13**, 53–65.
- Schork, M. A. & Remington, R. D. 2000: *Statistics with Applications to the Biological and Health Sciences*, 3rd edn. Prentice Hall, Upper Saddle River, NJ.
- Schuler, K. L., Leslie, D. M., Shaw, J. H. & Maichak, E. J. 2006: Temporal-spatial distribution of American bison (*Bison bison*) in a tallgrass prairie fire mosaic. *J. Mammal.* **87**, 539–544.
- Schwartz, C. C. & Hundertmark, K. J. 1993: Reproductive characteristics of Alaskan moose. *J. Wildl. Manage.* **57**, 454–468.
- Shaw, J. H. & Carter, T. S. 1989: Calving patterns among American bison. *J. Wildl. Manage.* **53**, 869–898.
- Singer, F. J. & Zeigenfuss, L. C. 2002: Influence of trophy hunting and horn size on mating behavior and survivorship of mountain sheep. *J. Mammal.* **83**, 682–698.

- Smith, D. W., Mech, L. D., Meagher, M., Clark, W. E., Jaffe, R., Phillips, M. K. & Mack, J. A. 2000: Wolf-bison interactions in Yellowstone National Park. *J. Mammal.* **81**, 1128–1135.
- Towne, E. 1999: Bison performance and productivity on tallgrass prairie. *Southwest. Nat.* **44**, 361–366.
- Underwood, R. 1982: Vigilance behaviour in grazing African antelopes. *Behaviour* **79**, 81–107.
- Van Vuren, D. 1983: Group dynamics and summer range of bison in southern Utah. *J. Mammal.* **64**, 329–332.
- Weckerly, F. W. 1998: Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J. Mammal.* **79**, 33–52.
- Whittle, C. L., Bowyer, R. T., Clausen, T. P. & Duffy, L. K. 2000: Putative pheromones in urine of rutting male moose (*Alces alces*): evolution of honest advertisement? *J. Chem. Ecol.* **26**, 2747–2762.
- Wilson, G. A., Olson, W. & Strobeck, C. 2002: Reproductive success in wood bison (*Bison bison athabasca*) established using molecular techniques. *Can. J. Zool.* **80**, 1537–1548.
- Wolff, J. O. 1998: Breeding strategies, mate choice, and reproductive success in American bison. *Oikos* **83**, 529.
- Wyman, T. 2002: Grizzly bear predation on a bull bison in Yellowstone National Park. *Ursus* **13**, 375–377.
- Zar, J. H. 1999: *Biostatistical Analysis*. Prentice-Hall, Upper Saddle River, NJ.