

Bellows, copulations, and sexual selection in bison (*Bison bison*)

We provide data on the timing and frequency of bellowing episodes and 261 copulations in North American bison (*Bison bison*) extracted from more than 8500 h of observation to examine Darwin's idea that by using breeding-season vocalizations the male "endeavours thus to charm or excite the female." Copulatory status affected vocalization rates; after mating, the frequency of male bellowing dropped to 16.1% of precopulatory rates ($p < .0001$). Males bellowed at a higher rate on days when females were in estrus ($p < .025$) than when they were in anestrus, but females' probability of offspring production in the next year was not correlated with bellowing rate. For estrous females, bellowing was positively correlated with number of attendant males ($p < .0001$) and inversely related both to the number of days individual males had participated in the rut ($p < .05$) and to the date during the 6-week breeding season ($p < .003$). Body size also influenced bellowing rate: with other factors held constant, small males bellowed more than large males ($p < .03$). With respect to Darwin's idea that vocalizations serve as a male display to females, (1) males bellowed neither before nor after copulating when rivals were absent but (2) they bellowed both before and after copulating when rivals were present. Overall, these results suggest that bison bellows do not serve as advertisements to females but function as intrasexual displays. [*Behav Ecol* 1991;2:1-6]

Darwin (1872) suggested that "the sexes of many animals incessantly call for each other during the breeding season; and in not a few cases, the male endeavours thus to charm or excite the female," a premise now supported for some anurans (Andersson, 1982; Arak, 1983; Ryan, 1985), insects (Thornhill and Alcock, 1983), and birds (Gibson and Bradbury, 1985). Darwin's "advertisement to female" hypothesis has not been rigorously examined in mammals, in part because of complexities of mammalian mating systems (Clutton-Brock, 1989; Eisenberg, 1981) and because of difficulties in separating the potential effects of male-male competition from those of female choice (Bateson, 1983; Bradbury and Andersson, 1987; Clutton-Brock et al., 1979). However, there is evidence that breeding-season vocalizations by male ruminants may accelerate estrus (McComb, 1987), discourage rivals (Bowyer and Kitchen, 1987; Clutton-Brock and Albon, 1979), and deter predators and maintain spatial proximity to mates (Tilson and Norton, 1981). Although vocal communication among ungulates is widespread (Kiley, 1972) and the sounds of cattle have received considerable study (Hall et al., 1988), except for red deer (Clutton-Brock and Albon, 1979; McComb, 1987), few

of the functions of vocalizations have been investigated.

Among sexually dimorphic mammals, males are polygynous and would not be expected to maintain prolonged consortships with females after mating (Kleiman, 1977) unless sperm competition occurs (Foltz and Schwagmeyer, 1989; Ginsberg and Huck, 1989; Hogg, 1988). Because males of nonharem-holding species often terminate their guarding of females after copulating (Berger, 1986; Lott, 1979), it should be possible to make inferences about functions of male displays by contrasting their behavior before and after mating. For instance, if male calls are advertisements to females, then males should vocalize to females before mating but not after, whether or not conspecific rivals are present. Mammals have been particularly problematic for investigations of this sort because most species are nocturnal, small, and difficult to observe. The visible species that copulate in the open, such as fallow deer (*Cervus dama*) or wild horses (*Equus caballus*) (Apollonio et al., 1989; Berger, 1986) are not particularly prone to conspicuous vocal episodes.

North American bison (*Bison bison*) are an interesting species in which to examine the function of breeding-season vocalizations. Bi-

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son are the largest terrestrial mammals of the New World (Eisenberg, 1981), occurring in large groups in open habitats. Their mating system differs from most ungulates. Unlike some species in which males defend harems either seasonally (deer: Clutton-Brock et al., 1982) or year-round (equids: Berger, 1986) or in which they defend mating territories (antelopes: Gosling, 1986), male bison form ephemeral (usually less than a day) associations with females who are guarded against 1–16 attendant males, employing both agonistic and vocal behavior (Lott, 1979, 1981). Female bison usually mate only once (Lott, 1979), and on North America's relatively treeless prairies copulations are observable events, with the most successful males in a given year copulating with up to 14 females (Berger J, in preparation). After mating, females erect their tails in a conspicuous upright posture for up to 6 h, making it relatively easy to identify when animals have been bred and to quantify differences in male pre- and postcopulatory behavior. Evidence of male, but not female, mate choice exists. Males show a preference for females with a higher probability of calf production in the next year; these tend to be better-conditioned females and include nonlactating cows (Berger, 1989). Male bison move over large areas during the rut, traveling up to 33 km a day in search of females, even though more than 85% of the mature males may actually spend less than 2 weeks in habitats where females occur during the 6-week rut (Berger, 1989). Bellowing is a conspicuous breeding-season characteristic (Lott, 1974), described nearly 150 years ago as "the long continued roll of a hundred drums" (Audubon, 1843, cited in Cates, 1986). Bellows are short (mean = 2.05 s), guttural, low-frequency (mean = 230 Hz) exhalations (Gunderson and Mahan, 1980) that occur when males are alone, in mixed-sex groups, and, most often, with females.

Because males bellow when guarding females and when confronting rival males, it is important to specify the conditions in which bellowing might support or reject a female advertisement or a male–male competition hypothesis, although both could ultimately be responsible for male bellowing. The female-advertisement hypothesis predicts that males should bellow before copulating but not after and that bellowing should be independent of the presence of rival males. The male-deterrence hypothesis predicts that bellowing should occur only in the presence of rivals, irrespective of the timing of copulations. In this paper we examine breeding-season vocalizations of bison in relation to the presence of rival males and the timing of copulation. Our data set permits statistical control for a

number of confounding variables and provides a necessary first step toward a better understanding of the role of vocal advertisement in mammalian sexual selection.

METHODS

We studied bison in Badlands National Park, South Dakota, USA (40°50' N, 102°20' W) from 1985 to 1989. At Badlands, bison were neither artificially fed nor restricted in their movements during the first 4 years of study. The park (250 km²), although small relative to areas used by bison historically, is the largest shortgrass preserve with bison in North America. We collected data during all months of the year; from May until mid-August each year we made daily observations, and from July to August we made observations during every hour when it was light enough to see. The information reported here is based on more than 8500 h of observation and on evidence of 261 copulations. More than 200 animals were known individually based on ear tags, brands, and combinations of distinguishable head hair and horn patterns. Throughout the study more than 1200 animals were handled through capture operations that involved immobilization or driving animals into a fenced area where they were weighed on cattle scales, aged, and checked for morphological measures (Berger, 1989; Berger and Peacock, 1988; Green and Berger, 1990; Kock and Berger, 1987).

Because our studies focused on reproductive success (Berger J and Cunningham C, in preparation), initially observations were on focal consorts in which both members of a dyad were known. Observations continued until males either copulated with or departed from the female. We noted the number of males occurring within 15 m of the pair and their identities (when known), as well as the frequency of threat and contact interactions and displacements. In situations in which only one member of a dyad was identifiable, observations centered on known males. Some data are included from unknown males who copulated, but these represent less than 20% of the total. We determined the reproductive status of females by noting whether they were nulliparous, barren, or lactating, the latter by presence of a distended, swollen udder.

We recorded the frequency of bellowing for focal males with mechanical counters both before and after mating. We adopted standard 30-min periods, but, because animals occasionally moved out of view or consorted for shorter amounts of time, the frequency of bellowing was averaged per 30 min, a value we designated as the bellowing rate. Our analyses are based on bellowing data for focal males,

both those who copulated or were unsuccessful, and include bellowing rates for breeding males subdivided into periods before and after copulation. Thus, if male X guarded a female for 120 min, copulated, and remained for an additional 15 min, his bellowing rate would reflect the actual frequency of bellows until copulation, and postcopulatory bellows would be scaled to the first 30-min postcopulatory period. Postcopulation data were omitted if males did not remain for at least 10 min. For males who did not copulate but remained in consort with females during observation periods, data were used in contrasts of bellowing rates of breeders versus nonbreeders.

We adopted the following definitions: *Attendant male group size* refers to the number of males occurring within 15 m of the consort pair, assuming a male bison to be 3 m in length. Since the membership of attendees was not constant over observation periods, we recorded the number of males present at 5-min intervals and then computed an average per 30 min before and after copulation. *Copulatory status* refers to mated and unmated males. *Female reproductive potential* refers to the probability that a female produced a viable calf in the following year. These data were based on retrospective analyses of a female's actual reproductive performance over a multiple-year period. For instance, females lactating a calf in one year had a lower probability of producing offspring during the next year than did females that were barren in a given year (see Berger, 1989). *Interval to mating* is one of several 30-min time periods before copulation. Time at copulation is zero, and periods before are indicated by a negative value (e.g., -30 min is 30 min before mating), whereas postcopulatory periods have positive values (see Figure 1). *Days at rut* reflect the number of different days that males associated with female groups. Throughout the rest of the year adult males were sexually segregated and used different habitats from females (Berger J, unpublished data).

We used multivariate methods to partial out the effects of specific variables and log transformed the data to meet assumptions of normality (Sokal and Rohlf, 1981). To avoid problems of pooling data where more than one individual contributes differentially to the total sample, either we matched pairs of individuals where both contributed equally (such as males of different body size) or we used data from single estrus events of females, avoiding using some males multiple times and others just once. However, in some circumstances we pooled data on male bellowing rates; for instance, we used mean values for all males who consorted with females in the general comparison of precopulatory versus

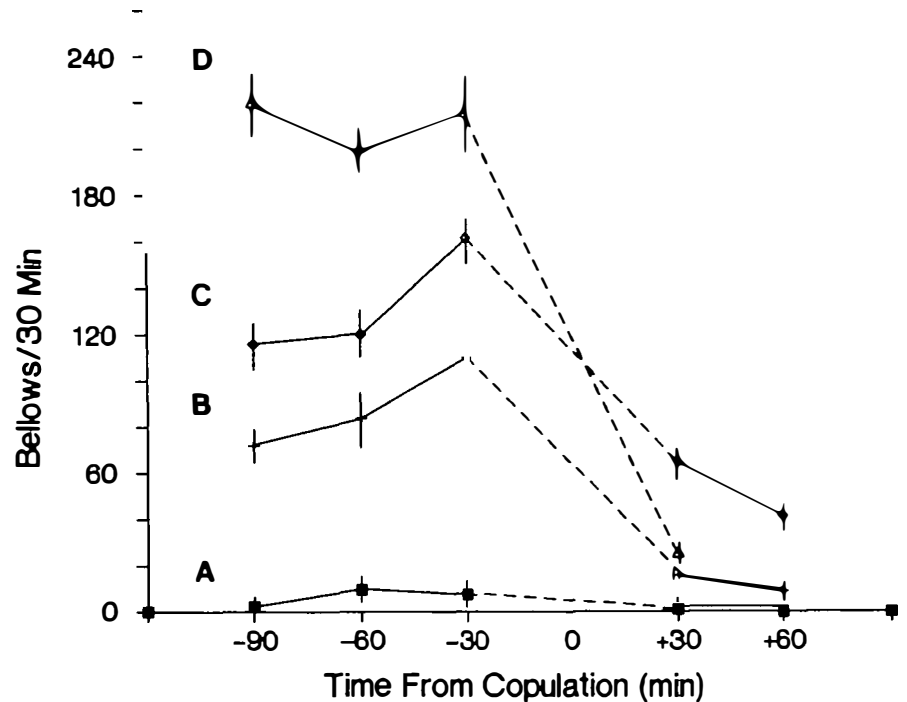


Figure 1
Relationship between time from copulation and mean bellowing rate (\pm SE) for consort males with different numbers of attendant males: (A) <1; (B) 1–3.99; (C) 4–7.99; (D) \geq 8. Sample sizes for each attendant male group size at -90, -60, -30, +30, and +60 min are: (A) 7, 7, 9, 7, 3; (B) 18, 17, 15, 18, 9; (C) 9, 18, 26, 16, 11; (D) 4, 5, 10, 7, —.

postcopulatory bellowing rates, and this may affect our interpretations to an unknown extent.

RESULTS

The frequency of bellowing varied among individuals from 0 to 956/h and up to 3272 for a 4-h period. Interval to mating, attendant male group size, and copulatory status all affected bellowing rates (Figure 1). The single most important variable that affected bellowing rate was copulatory status. Postcopulatory rates were only 16.1% of precopulatory rates (three-way factorial ANOVA: $F_{3,215} = 345.85$, $p < .0001$).

Attendant male group size was also highly significant ($F = 265.60$, $p < .001$). When groups of eight or more males were present, bellowing rates were approximately 60% higher than when male group size was four to eight. However, when males consorted with females away from others, bellowing rates dropped. For instance, of nine observed copulations when females were sequestered (e.g., not in view and at least 1 km away) from other males, bellows averaged less than 7.7 per 30 min in contrast to 110 per 30 min when one to four males were present. [The binomial probability of nine males having the fewest bellows/period in the 0–0.99 category of attendant males (from Figure 1) is 0.000038.] Bellowing dropped precipitously within 2 min after attendant males left a consorting pair (Wilcoxon matched-pairs test: $T_s = 10.5$, $n = 19$, $p < .01$). As time to mating decreased,

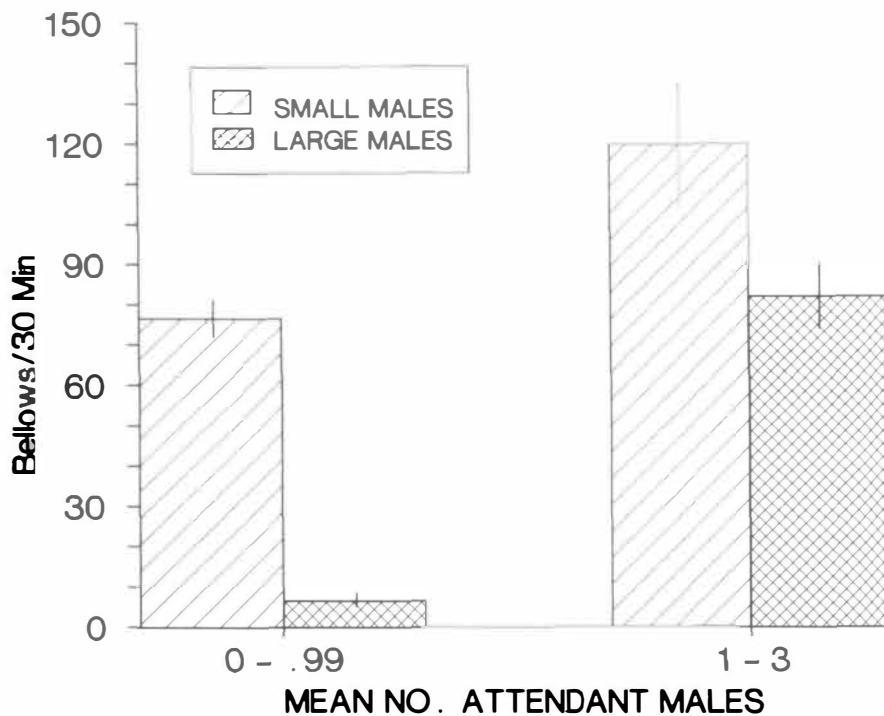


Figure 2
Relationship between mean bellowing rate and equal-aged small and large males with different numbers of attendant males on days when females were not in estrus. Small and large males, matched by age (5, 7, and 9 years old), were contrasted with two and four replicates of each bellowing male while guarding anestrus females with 0–0.99 and 1–3 attendant male categories. Means (\pm SE) are indicated.

bellowing rates of males with attendant males of intermediate group size increased, presumably because precopulatory guarding entailed thwarting the advances of potential rivals, which was accomplished by increased bellowing rates. Evidence that supports this notion is the inverse relationship between bellowing rate and the number of social interactions/min/male ($r_s = -.37$, $df = 62$, $p < .017$). The absence of a relationship between bellowing rate and duration of precopulatory consortships ($r_s = -.19$, $df = 62$, ns) suggests that males do not necessarily enhance their associations with females by increased vocalizations. The overall effect of interval to mating was highly significant ($F = 12.34$, $p < .001$) and remained significant when effects of increased male attendance were partialled out ($r_{\text{partial}} = .20$, $p < .05$).

At least three additional factors may affect bellowing rates. First, adult males enter the rut at different periods throughout the summer, participating for different lengths of time (Berger, 1989). If some males had participated in the rut for 12 days and others for only two or three, direct comparison might confound interpretation because bellowing rates may have been reduced in the former due simply to fatigue. Second, because females vary in their reproductive potential (Berger, 1989), consort males might bellow more in defense of those with a higher probability of calf production. Third, bellowing rate may vary seasonally, independent of other factors. We explored these possibilities with multiple regression, explaining 60% of the variance in

precopulatory bellowing rates ($F = 44.62$, $df = 93$, $p < .0001$), with $Y = 0.994 + 0.696X_1 - 0.019X_2 - 0.017X_3$, where X_1 = attendant males, X_2 = days at rut, and X_3 = date. Second-order partial correlation coefficients for these are .74 ($p < .0001$), $-.21$ ($p < .05$), and $-.31$ ($p < .003$). Female reproductive potential had no effect.

However, if males competed more for estrous females than they did simply to consort with females irrespective of estrus state, then bellowing should be greater on days when females were in estrus. For instance, less than 10% ($n = 121$) of 1400 consortships led to copulations (Green and Berger, 1990) although more than 75% involved bellowing. Analysis of variance revealed that both estrous state and attendant male group size independently affected bellowing rates ($F_{\text{group size}} = 9.93$, $df = 76$, $p < .0001$; $F_{\text{status}} = 6.70$, $p < .025$), indicating that males did not bellow as intensively when females were not in peak estrus.

Additionally, because males of many species employ alternative tactics to enhance chances of mating (Berger, 1986; Howard, 1978; Sherman, 1989), some of which are related to body size, we asked whether body mass influenced bellowing and compared small- with larger-bodied males. Age, seasonal (e.g., date), and copulatory status effects were controlled by contrasting evenly matched, same-aged but different-sized males during a 9-day period in mid-July 1988 when none had copulated. The mean body mass of three large males (797 kg) was significantly different from that of three smaller males (705 kg; $t = 4.99$, $df = 4$, $p < .01$). Bellowing rates for smaller males were about 185% higher (Figure 2), with body size exerting a stronger effect than the number of attendant males on bellowing (ANOVA_{2,35}; $F_{\text{body size}} = 5.60$, $p < .03$; $F_{\text{group size}} = 3.68$; the interaction was not significant).

DISCUSSION

The data are inconsistent with the idea that males advertise to females because males rarely vocalized when other males were absent (Figure 1). Had bellowing occurred when females were sequestered from other males, an epigamic function for bellowing might seem reasonable, but the positive relationship between bellowing rate and male group size favors the belief that the male vocalizations serve an intrasexual function. Nevertheless, difficulty remains in teasing apart potential intrasexual and intersexual roles. Perhaps males bellow when other males are present simply to provide females with a more direct and simultaneous choice, but this is an unlikely scenario because males bellow to one another

even when females are absent. Additionally, the strikingly abrupt cessation of bellowing after copulation, irrespective of the number of attendant males (Figure 1), indicates a strong effect of rival males, although it remains unclear why postcopulatory bellowing drops to only 16% of precopulatory rates. If sperm competition occurred, there would be no reason to expect dramatic differences between pre- and postcopulatory bellowing rates, assuming that rivals do not depart and that bellowing coupled with active aggression by mated males deters the advances of rivals. While our methods of data collection accounted for the number of attendant males present both before and after copulation, we did not gather data on the bellowing rates of attendant rivals. It is possible that rival males changed components of their behavior (including a reduction in bellowing) due to the copulation per se. If so, then the males who copulated may have altered their vocal behavior in response to an undetected or unmeasured variable that rendered rivals as less competitive. Alternatively, the drop in bellowing rate after copulation may have occurred simply because rivals posed a reduced threat.

Why small males bellow more is unclear. If diminished breeding opportunities were compensated for by increased vocalizations and smaller males successfully copulated, support for an epigamic function might be gained simply because small males advertised more. Although none of the smaller males copulated in 1988, perhaps their high vocal rates serve to intimidate (future) rivals. Alternatively, high vocal rates in nonbreeding subordinate males may be a nonadaptive consequence of small size.

Information for deer (Clutton-Brock and Albon, 1979; McComb, 1987), birds (Gibson and Bradbury, 1985), and anurans (Arak, 1983; Ryan, 1985) suggests that the breeding-season sounds made by males function as both intrasexual displays and epigamic ones, the latter either by serving as markers of condition or by advertising other components of potential fitness. A unique feature of the data reported here is that predictions about vocal functions were examined within the pre- versus postcopulatory framework while controlling for effects of potentially confounding proximate variables. The evidence we report offers a reasonably sound refutation of a potential epigamic function for breeding-season bellows in bison. Other studies of ungulate vocalizations have generally been descriptive (e.g., Gunderson and Mahan, 1980; Kiley, 1972), neither placing their findings in a hypothesis-testing mode nor examining them in the context of sexual selection. While the pre- versus postcopulatory framework has not been

used previously, principally because data on mating in other mammals in relation to vocalizations have been lacking, it cannot by itself refute all possible scenarios. For instance, while we demonstrate that attendant male group size affects the bellowing rates of males guarding estrous females, males may still need to vocalize when females are sequestered from other males because the females remain unconvinced about the prowess of their male consorts. Additionally, the infrequent bellowing rates we reported for sequestered pairs may be sufficient to provide females with the necessary information to make a choice, perhaps through characteristics of the bellows themselves rather than bellowing rate per se. Finally, we do not rule out the possibility that male bison impress females through fighting or scent urination involving urine metabolites (Coblentz, 1976) or other olfactory processes (Blaustein, 1981). Nevertheless, our data on the rate of bellowing episodes (1) are inconsistent with the notion that breeding-season vocalizations serve as advertisements to females, a suggestion with indirect support based on song data of several primates (Mitani, 1988; Sekulnic, 1982); (2) highlight some of the more straightforward findings that emerge when controlling for numerous sources of bias; and (3) suggest that female bison do not evaluate their fellow's bellows.

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