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# Amplitude of bison bellows reflects male quality, physical condition and motivation

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Sound amplitude (measured as sound pressure level) is an acoustical parameter that has received little attention within communication research, especially in mammals. Although difficult to measure in the field, amplitude is a potentially important parameter of sexually selected signals. In North American plains bison, *Bison bison*, 'bellows' are low, guttural vocalizations made by bulls during the breeding season in the context of male–male contests. It has been hypothesized that bison use bellow amplitude to assess males during male–male competition or female mate choice. In this study, we tested the hypothesis that amplitude is significantly related to measures of bull competitive ability (quality, condition and motivation), and thus, could function as a sexually selected signal. During peak rut over 2 years, courtship and threat behaviours were recorded daily. During observation sessions, bellow amplitude was measured as peak sound pressure levels using a sound level meter. Subsequent genetic parentage analysis determined offspring sired by males. Based on aspects of signalling and game theory, we predicted positive associations between amplitude and mating and reproductive success, dominance, physical condition, motivation to retain females, age and weight. Our results supported a positive association between amplitude and both physical condition and motivation. Conversely, the results showed a negative association between amplitude and quality, as measured by mating and reproductive success. Supporting evidence and alternative hypotheses for these results are explored. Our findings provide support for the notion that bellow amplitude could be used as a sexually selected signal to assess rival males during male–male competition.



*Keywords*: amplitude; bison; *Bison bison*; condition; loudness; male quality; motivation; sexual selection; sound pressure level

Sexual selection arises from differences in reproductive success driven by male–male competition and mate choice (Darwin 1871; Andersson 1994). An array of attributes, often sexually dimorphic, may generate signals containing information about the individual's competitive ability, quality or sexual receptivity. Both senders and receivers attempt to use these signals to maximize their own reproductive success (Owings & Morton 1998). Signals can evolve to be reliable or 'honest' if there are costs and constraints to the sender that make conveying truthful information a more optimal strategy than lying (Zahavi 1975; Grafen 1990; Zahavi & Zahavi 1997; reviewed in Vehrencamp 2000; Hurd & Enquist 2005).

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Vehrencamp (2000) defined signal types based on these costs and constraints: 'index' signals cannot be faked because of physical or physiological constraints; 'handicap' signals are more reliable because of production costs or increased vulnerability of attack by inter- or intraspecific receivers; and 'conventional' signals, while not risky or costly to produce, are kept honest by the threat of receiver retaliation. Generally, males with high quality, condition or motivation produce more intense, costly signals because they can bear, or are willing to bear, the costs of these signals more than males with low quality, condition or motivation.

Acoustic signals can encode and transmit a variety of biologically significant information such as species, gender, individual identity, age, size, physical condition, competitive ability, mating success, reproductive success and motivational state (Bradbury & Vehrencamp 1998). Most studies of sexually selected signals have focused on temporal and spectral call characteristics, neglecting call amplitude despite its importance in animal signalling. Amplitude is difficult to measure, especially in the field as it is susceptible to attenuation and degradation (Wiley & Richards 1982). This parameter is important because it has the ability to be a significant sexually selected signal that remains underexamined.

Amplitude levels at the source determine the active space of a vocalization (range over which the signal is audible to receivers), along with transmission loss and receiver detection thresholds (Marten & Marler 1977). Generally, louder calls can travel farther and be detected more clearly by receivers over background noise. Animals can regulate amplitude in relation to different social contexts. Playback experiments show that males increase call amplitude in response to playbacks of female or rival male calls (anurans: Lopez et al. 1988; birds: Cynx & Gell 2004) and that alarm call volume can influence receiver behavioural responses (mammals: Blumstein & Armitage 1997). Zebra finches, *Taeniopygia guttata*, can adjust call amplitude relative to intended receiver distance (Brumm & Slater 2006). Such experiments imply that amplitude could be important in social interactions.

Signal amplitude has the potential to function as an honest indicator of quality, competitive ability, condition or motivation if increased amplitude results in costs to the sender, such as increased energetic expenditures (Russell et al. 1998) and attraction of intraspecific (e.g. rival males) or interspecific (e.g. predators or parasites) eavesdroppers (McGregor & Dabelsteen 1996; Gil & Gahr 2002). Amplitude can also be physically constrained by body size (Titze 1994; Fitch & Hauser 1995), with larger animals potentially capable of producing louder calls (documented in insects: Forrest 1983; anurans: Gerhardt 1975; Arak 1988).

During male–male competition, males may use amplitude to repel rival males or defend territories. Increased call amplitude has been associated with increased dominance rank, aggression and/or displacement events (Kroodsma 1979; Dabelsteen 1981; Todt 1981; Sanvito & Galimberti 2003). In red deer, *Cervus elaphus*, louder 'harsh roar' call types appear to be associated with very high rut activity, including roaring contests and repeated herding (Reby & McComb 2003). Typically, call amplitude increases in response to the presence of rival males in anurans (Lopez et al. 1988) and birds (Brumm & Todt 2004), but in close aggressive encounters, low-amplitude calls can sometimes predict a higher likelihood of attack in birds (Searcy et al. 2006).

Amplitude of male calls may also attract females and influence mate choice. Female insects, birds and anurans are more attracted to louder calls or stridulations (Walker & Forrest 1989; Searcy 1996; Castellano et al. 2000) with a difference as small as 2–3 dB influencing mate choice (review in Gerhardt & Huber 2002). Female preference for louder calls may indicate a 'passive attraction' for the closer perceived caller, but females can also show 'active choice' by differentiating between caller effort and location and choosing the more powerful but distant call even when perceived intensities are similar (Castellano et al. 2004).

Previous research on the amplitude of airborne vocalizations within sexually selected interactions has focused on insects, birds and anurans rather than large mammals in the field, with one partial exception. Sanvito & Galimberti (2003) studied associations between amplitude and age, size and breeding status in elephant seals, *Mirounga leonine*, but did not examine more detailed measures of physical condition, fighting ability, reproductive fitness or motivation.

This paper evaluates the role that bellow amplitude may play in sexually selected interactions of a large sexually dimorphic mammal, the North American plains bison, *Bison bison*. Bellow vocalizations are loud, low-frequency male-specific calls given in the context of the rut. Bellows are most actively used in relatively short-distance communication with challenging males typically 5–10 body lengths apart, although rival males may be attracted to bellowing bulls and their potential females from greater distances. The costly nature of bellowing is suggested by the observation that bellowing rates decrease with increasing time spent in the rut, attributed to fatigue by Berger & Cunningham (1991), and that time spent bellowing reduces time spent foraging or resting (Mooring et al. 2006). Producing louder vocalizations during the breeding season could entail potential costs and constraints to the sender through intense contraction of abdominal and lateral muscles and saliva loss associated with frequent bellowing (Wolff 1998). When the muscles used for fighting are also used during frequent, intense threat vocalizations, these vocalizations may provide important information about the fighting ability or stamina of the individual (Bradbury & Vehrencamp 1998). In addition to energetic costs, increased bellow amplitude would expand the active space of these vocalizations, increasing the likelihood of attracting rival males.

It has been hypothesized that bison bellows are sexually selected signals used by bison to assess males during male–male competition or female mate choice (Berger & Cunningham 1991; Wolff 1998). Given the potentially costly nature of increased bellow amplitude, we predicted that bellow amplitude would vary with factors associated with male competitive ability (quality, physical condition and motivational state). Based on evolutionary game theory and assuming bellow amplitude is subject to production costs, constraints and risks, we predicted positive