

NORTH AMERICAN ELK BUGLE VOCALIZATIONS: MALE AND FEMALE BUGLE CALL STRUCTURE AND CONTEXT

J. A. FEIGHNY, K. E. WILLIAMSON, AND J. A. CLARKE*

School of Biological Sciences, University of Northern Colorado, Greeley, CO 80639, USA

Bugle calls of male North American elk (*Cervus elaphus*) are common sounds during fall in the Canadian and United States Rocky Mountains. In contrast, bugle calls of female elk are rarely heard. We quantified the acoustic structure of elk bugle calls, which is an essential 1st step to understanding of the function of the call. We also investigated whether motivation–structural rules apply to these long-distance calls. We measured male elk bugle calls in Rocky Mountain National Park, Colorado, during autumn of 1998 and 1999 and we measured female elk bugle calls on 2 Colorado elk ranches (private establishments that raise elk for commercial purposes) during spring of 2001 and 2002. All bugle calls had 3 segments: on-glide, whistle, and off-glide. Male bugle calls were longer in duration than female bugle calls ($P < 0.01$). Bugle calls emitted in aggressive interactions had 4 or 5 low-frequency formants, resulting in harsher, wider bandwidth bugles ($P < 0.001$) compared to the tonal calls emitted in nonaggressive contexts, which lacked formants. Thus, elk bugle calls appear to conform to motivation–structural rules.

Key words: bugle call, *Cervus elaphus*, communication, motivation–structural rules, North American elk, wapiti

The breeding season calls of red deer (*Cervus elaphus*) stags have been meticulously quantified, particularly the “roar” vocalization (Clutton-Brock and Albon 1979; Kiley 1972; McComb 1987, 1991; Reby et al. 2001; Reby and McComb 2003). Roars of red deer stags typically exhibit 3 phases caused by changes in vocal fold vibration and vocal tract shape (Fitch and Reby 2001; McComb 1987; Reby 1998): 1st an increase in the fundamental frequency with numerous formant frequencies; a 2nd phase with low formant frequencies but high fundamental frequency, high amplitude, and often chaotic noise; and a final brief phase of increasing formants and falling fundamental frequency and amplitude (Reby and McComb 2003).

Similar to red deer, North American elk (also *C. elaphus*) are polygynous and exhibit male–male competition involving visual and vocal displays and the formation of female harems with 1 dominant male during the fall breeding season (Clutton-Brock et al. 1982; Murie 1932, 1951). During the breeding season, male elk emit bugle calls that have been proposed to function in attracting potential mates, bringing herd members closer together, and aiding in the assessment of fighting ability and dominance of other males (Bowyer and Kitchen 1987; Clutton-Brock et al. 1980; de Vos et al. 1967; Geist 1982;

Struhsaker 1967). Female elk also have been noted to bugle but it is a rare event, occurring in the spring during the weeks when parturition occurs (Murie 1932). In spring, adult males disperse until the following mating season, whereas females remain in matriarchal herds of 10–30 adults and their yearling young (Bowyer and Kitchen 1987). Although descriptive accounts exist regarding male elk bugle calls, quantitative measures are lacking regarding the acoustic structure of the call and no descriptions exist regarding the rarely heard female elk bugle call.

The 1st goal of our study was to quantify and compare the acoustic structure of the bugle call emitted by male and female elk. Our 2nd goal was to investigate the hypothesis that the acoustic structure of elk bugle calls varied with the behavioral context in which calls were emitted and conformed to motivation–structural rules. Motivation–structural rules predict that aggressive vocalizations are low-frequency, wide-bandwidth sounds, whereas fearful or friendly (appeasing) vocalizations are high-frequency, narrow-bandwidth sounds (Morton 1977). These rules are based on the hypothesis that selection favors the use of harsh, low-pitched sounds in hostile contexts because these sounds indicate a large body size and thus convey a greater threat (Darwin 1871; Hauser 1996; Morton 1977). Selection also may favor the use of tonal, higher pitched sounds in friendly or fearful contexts because these sounds indicate a smaller sized or immature individual, thus denoting little threat (Darwin 1871; Hauser 1996; Morton 1977). These descriptions represent endpoints of a vocal behavioral spectrum, which has been studied extensively in

* Correspondent: jennifer.clarke@unco.edu

TABLE 1.—Means and ranges for duration, lowest fundamental frequency, highest fundamental frequency, and peak (loudest) fundamental frequency of the on-glide, whistle, and off-glide segments of male elk (*Cervus elaphus*) bugle calls in Rocky Mountain National Park, Colorado ($n = 10$ male elk, 1–3 calls/bull).

	On-glide	Whistle	Off-glide
Duration (s)	0.75 (0.18–1.27)	1.31 (0.84–1.95)	0.31 (0.09–0.47)
Low frequency (kHz)	0.69 (0.24–1.62)	1.74 (1.44–2.18)	0.41 (0.02–1.24)
High frequency (kHz)	1.90 (1.41–2.35)	2.08 (1.65–2.55)	1.95 (1.62–2.26)
Peak frequency (kHz)	1.24 (0.52–2.11)	1.90 (1.46–2.28)	1.08 (0.17–1.89)

various species of mammals (August and Anderson 1987; Compton et al. 2001; Harrington 1987; Morton 1977, 1982). Morton (1977) originally proposed motivation–structural rules for close-proximity vocalizations; however, he noted that these rules might apply to the long-distance calls of social species. We (JAC, JAF) have observed that elk bugle calls propagate for up to a kilometer or more depending on habitat and terrain. Acoustic qualities of bugle calls may allow rival males to assess the willingness of a male to engage in a fight, a male's potential fighting abilities, or both. We predicted that acoustic qualities of the bugle call would differ with the context and sender's motivation.

MATERIALS AND METHODS

Subjects and study sites.—We observed a wild population of elk during the fall breeding (rutting) season, September–October 1998 and 1999, in Rocky Mountain National Park, Colorado. We recorded male elk bugle calls ($n = 10$ male elk) at dusk between 1830 and 2000 h, <200 m from the bugling male and his herd. We used antler form and branching pattern to identify individual males and we selected males who had herds (master bulls). Antler branching patterns are individually distinct once a male elk reaches adulthood, similar to those in red deer stags (Clutton-Brock et al. 1982).

Female elk bugle calls ($n = 4$ females) were recorded during 2 spring calving seasons, May–June 2001 and 2002, at Harrington Elk Ranch and M & M Elk Ranch, Steamboat Springs, Colorado. Elk ranches are privately owned establishments that raise elk in large meadows for commercial purposes (e.g., meat, hides, antlers, and antler velvet). Female bugle calls were recorded between 1000 and 1300 h ≤ 100 m from the bugling individual. We identified individuals by their ear-tag numbers.

Behavioral observations.—Behaviors of focal (bugling) individuals and conspecifics were noted before, during, and after bugle calls were emitted to classify the context in which calls were emitted. Nonaggressive contexts for a master bull were when his associated herd was feeding in a relatively cohesive group (≤ 5 elk body lengths between herd members) and when no other adult males were seen or heard by the observers. Aggressive behavioral contexts for master bulls occurred when a potential rival male was seen or heard in the immediate vicinity of the master bull's associated herd, females were straying from the herd, a lone female approached the herd, and when a female avoided the master bull's mating advances. In each of these instances, herd cohesion was potentially threatened or mating by the male was thwarted. In this study, we used only observable male–male

interactions for aggressive contexts because of the explicit and unmistakable cause of aggression.

Nonaggressive contexts for female elk were when the all-female herds were quietly congregated while feeding or resting. All-female herds (with young of both sexes) are typical in the wild during the spring months when adult males are in bachelor groups. One bugle call was emitted in an aggressive context when a dominant female vocalized while actively chasing another female.

Acoustic characteristics and statistical analyses.—We analyzed the 19 clearest (low noise to signal ratio) male bugle calls emitted in nonaggressive contexts to determine general call characteristics ($n = 10$ male elk). Preliminary inspection of spectrograms revealed that nonaggressive bugle calls had 3 distinct segments and lacked formant frequencies. For each segment, we measured duration (s), lowest frequency (kHz), highest frequency (kHz), and peak (loudest) frequency (kHz).

We compared the 19 clearest male bugle calls ($n = 10$ male elk) and 12 female bugle calls ($n = 4$ female elk) emitted in nonaggressive contexts regarding duration (s), lowest fundamental frequency (kHz), highest fundamental frequency (kHz), and peak (loudest) fundamental frequency (kHz). The data sets each exhibited a normal distribution (Shapiro–Wilks test $P > 0.05$) and we used unpaired t -tests to determine if differences existed between the sexes in the measured call characteristics. Nominal significance level was initially set at $\alpha \leq 0.05$ and Bonferroni adjusted (Sokal and Rohlf 1995).

We compared 19 (low noise to signal ratio) male bugle calls emitted in nonaggressive contexts ($n = 10$ male elk, 1–3 calls/bull) with the 19 clearest (low noise to signal ratio) bugle calls emitted in aggressive contexts ($n = 9$ male elk, 1–3 calls/bull). We used the 2nd segment of bugle calls for statistical comparisons because it was the consistently clearest, loudest, and longest segment, allowing for more precise comparisons than the other segments. Propagation of the 1st and 3rd segments was often decreased because of the direction in which the bugling individual was facing or because of distance combined with wind. We also analyzed formant frequencies evident in the whistle portion of bugle calls emitted in aggressive contexts. The source–filter theory states that voiced signals are produced by laryngeal vocal fold vibrations (the source) that then pass through the supralaryngeal vocal tract, where they are filtered and produce peaks termed formants (Fant 1960). We used Praat 3.9.27 DSP package (P. Boersma and D. Weenink, University of Amsterdam, Amsterdam, Netherlands) to measure formant frequencies and spacing.

The data sets exhibited a normal distribution (Shapiro–Wilks test, $P > 0.05$) and paired t -tests were used to determine if differences existed between the contexts regarding duration (s), bandwidth, number of low harmonics, and number of high harmonics. Low and high harmonics were defined as harmonics less than and greater than the median frequency of the entire call, respectively. Nominal significance level was initially set at $\alpha \leq 0.05$ and Bonferroni adjusted (Sokal and Rohlf 1995).

Recording equipment and spectrogram analyses.—Recording equipment consisted of a Uher CR 160 AV tape recorder (Uher, Munich, Germany) for male calls, Sony TCD5 PROII tape recorder (Sony Corporation of America, New York, New York) for female calls, a Sennheiser K3-U microphone with a frequency response range from 50 Hz to 22 kHz (Sennheiser Electronics, Wedemark, Germany), and Maxell XL II 90 high-bias IEC type II audiotapes (Maxell Corp., Conyers, Georgia). To quantify acoustic characteristics of the bugles, we digitized waveforms, spectrograms, and spectrums using CANARY software version 1.2.1 or RAVEN (Cornell University, Ithaca, New York). We used a sampling rate of 22.1 kHz with 16-bit precision, a short-time Fourier transform math model of 1,024 points,

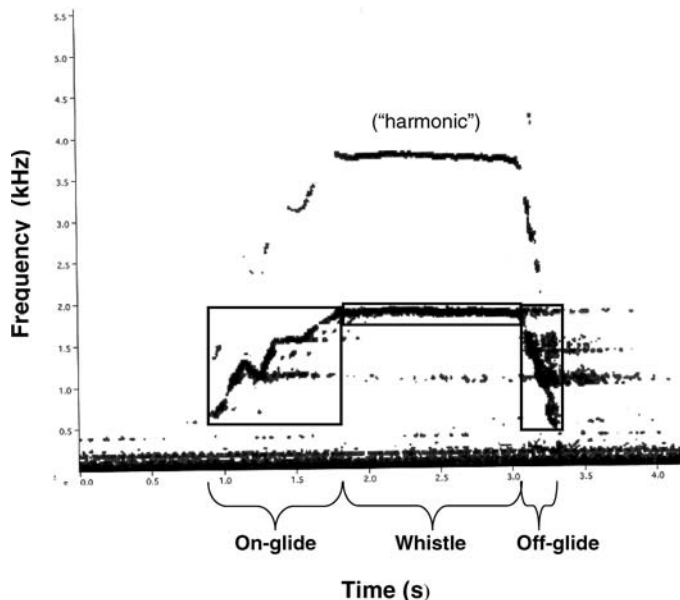


FIG. 1.—Three segments of a bugle call of a male North American elk (*Cervus elaphus*). Boxes indicate the on-glide, whistle, and off-glide. One harmonic is evident above the fundamental frequency in this call but the presence of harmonics varied with distance and the direction in which the individual was facing (echoes trailing off the off-glide at the end of the call are also evident in this CANARY spectrogram).

and a broadband filter spectrogram of 87.42 Hz with a frame length of 1,024 points. Grid resolution was 11.61 ms with 75% overlap and 21.53 Hz. A Hamming window was used for filtering.

RESULTS

General acoustic characteristics of elk bugle calls.—Bugle calls in nonaggressive contexts exhibited 3 main segments: an on-glide (gradual increase in sound frequency), a whistle (extended tonal frequency), and an off-glide (rapid decrease in sound frequency; Table 1; Fig. 1). The on-glide segment commenced with low frequencies and increased in frequency until it met with the onset of the whistle. The whistle segment was an extended, steady tone with the highest frequencies in the call. In the whistle segment, 1–3 harmonics were often evident above the fundamental frequency (F_0 = fundamental frequency). The whistle was followed by an off-glide, which was a rapid decrease in frequency, ending with the lowest frequencies of the call and followed by silence or by 1–5 grunts or yelps. Because bugle calls were followed by yelps in only 16% of 144 bugle calls recorded, we did not include an analysis of yelps in this study.

Comparisons between male and female bugle calls.—The general structure of female bugle calls was similar to that of male bugle calls regarding the presence of an on-glide, whistle, and off-glide (Figs. 2A and 3A). Average total call duration of the female bugle call (1.67 s) was less than that of male bugle calls (2.37 s; $t = 3.3927$, $d.f. = 29$, $P = 0.002$), and the on-glides exhibited more frequency modulations. No significant

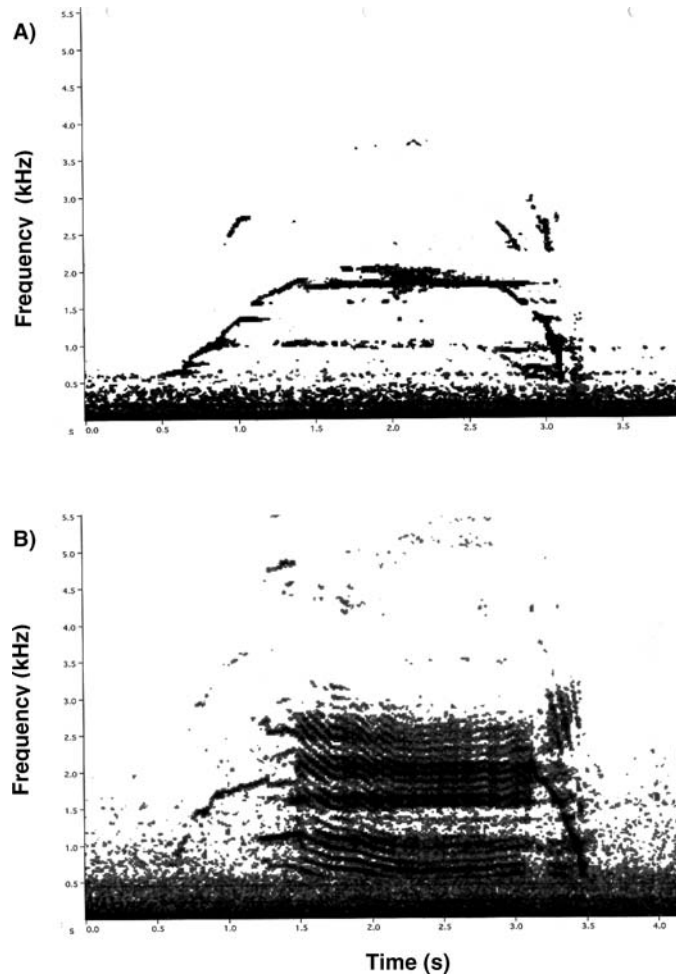


FIG. 2.—Comparison of bugle calls from a male North American elk in A) nonaggressive context and B) aggressive context showing wide bandwidth of whistle segment with low frequencies that are absent in the bugle call emitted in the nonaggressive context (CANARY spectrograms). Calls were recorded from the same distance from the male elk. (Increased noise floor in spectrogram B is due to increased vehicle traffic in Rocky Mountain National Park.)

differences existed between female and male bugle calls regarding lowest, highest, and peak (loudest) frequencies of the fundamental frequency ($P > 0.05$, all cases; Fig. 4).

Nonaggressive and aggressive bugle calls.—Bugle calls emitted by males in nonaggressive contexts (defined in “Materials and Methods”) had pure-tone qualities without formants. Bugle calls emitted in aggressive contexts with rival males were atonal (broadband, harsh sounding) with wider frequency bandwidths in the whistle ($t = 7.86$, $d.f. = 18$, $P < 0.0001$), more multiple, low-frequency harmonics ($t = 8.74$, $d.f. = 18$, $P < 0.0001$), and formants that ranged from an average minimum of 1,147 Hz in the 1st formant (F_1) to a maximum of 4,672 Hz in the 5th formant (F_5 ; Fig. 2B; Table 2). The spacing between the formants was as follows: F_1 – F_2 = 545 Hz, F_2 – F_3 = 532 Hz, F_3 – F_4 = 792 Hz, and F_4 – F_5 = 785 Hz. Formant spacing can convey information about body size (Riede and Fitch 1999).

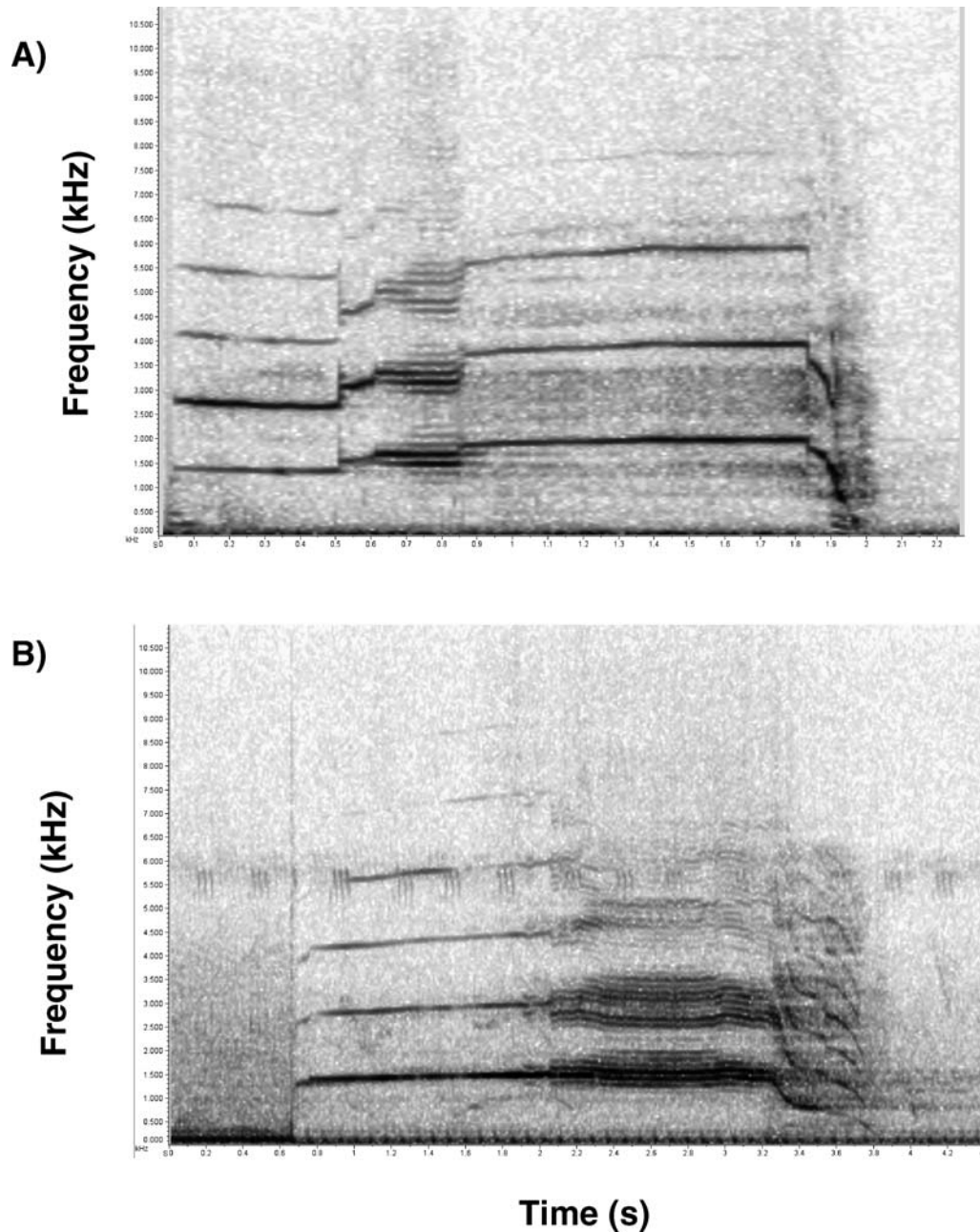


FIG. 3.—Comparison of bugles from a female North American elk in A) nonaggressive context (with on-glide harmonics that were not seen in male bugle calls) and B) aggressive context with low-frequency harmonics in whistle segment, similar to male bugle calls (RAVEN spectrograms). (Regularly spaced cricket chirps are present at ~ 5.50 kHz.)

The single bugle call emitted by a dominant female in an aggressive context (dominant female was chasing another female) was audibly and spectrographically similar to bugle calls emitted by males in aggressive contexts (Fig. 3B), but statistical comparisons are required before it can be stated that the calls are the same. The aggressive female bugle call was 3.16 s in duration for the total call (aggressive male bugle calls averaged 2.65 s) with a whistle low frequency of 1.17 kHz (aggressive male bugle calls averaged = 1.11 kHz), whistle high frequency of 2.00 kHz (aggressive male bugle calls averaged = 2.53 kHz), and >10 low-frequency harmonics.

DISCUSSION

Bugle calls of North American elk exhibit a stereotypic structure with 3 distinct segments. At this time we can only speculate regarding the function of each bugle call component based on its acoustic structure, but this speculation may indicate important directions for further investigations. The on-glide segment of the bugle call may serve as an alerting component and focus the receivers' attention on the sender because a rapid rise in sound frequency facilitates locatability (Marler 1967). We (JAC, JAF, KEW) have observed that the

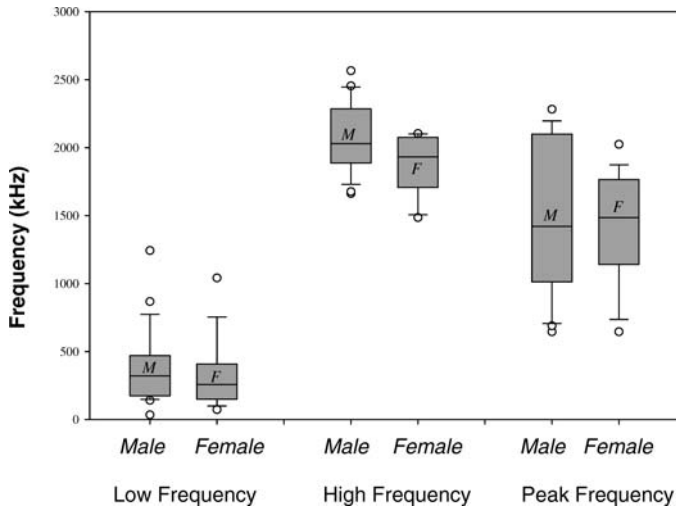


FIG. 4.—Comparisons of 19 bugle calls of male North American elk ($n = 10$ males) and 12 bugle calls of female elk ($n = 4$ females) emitted in nonaggressive contexts revealed no significant differences between the sexes in lowest, highest, and peak (loudest) frequencies of the total call fundamental ($P > 0.05$). Medians are plotted with 90th, 75th, 25th, and 10th percentiles.

whistle segment propagates the longest distances of bugle call segments and we suggest that this segment may function similar to “long calls” of adult male orangutans (*Pongo pygmaeus*) that mediate spacing among males (Mitani 1985). This potential function of the whistle is supported by our observation that bugle calls by a master bull appear to elicit bugle calls by nearby master bulls with harems that are out of sight, either on the opposite side of a hill or in another meadow separated by trees. Maintaining spacing between herds would be advantageous to a master bull to reduce the possibility of females “defecting” to another male’s herd. Because on-glide and off-glide segments do not propagate as far as the whistle, these segments may communicate with nearby herd members. The plosive yelps following a minority (16%) of bugle calls could represent a 4th segment of the bugle call. We are currently investigating whether bugle calls that conclude with yelps represent a graded vocalization between nonaggressive and aggressive bugle calls, similar to graded calls of white-nosed coatis (*Nasua narica*) that are followed by a plosive (Compton et al. 2001).

Bugle calls of females were similar in form to male bugle calls but differed in context, rate, and duration. Females bugled in the spring during late morning hours, whereas males bugled in the fall during dawn and dusk. Females emitted <1 bugle call/day whereas males emitted 1 or 2 bugle calls/min during the peak hours of calling. Bugling by female elk may be associated with high-stress periods and hormonal changes accompanying gestation and lactation, as proposed by Espmark (1964) regarding behavioral changes in female reindeer (*Rangifer tarandus*), but this aspect has yet to be investigated in elk. The duration of the female bugle call was shorter than that of the male bugle call, and at this point we can only speculate why this is the case. Shorter duration of the call may

TABLE 2.—Average minimum and maximum formant frequencies (Hz) of North American elk bugle calls emitted in aggressive contexts ($n = 9$ male elk, 19 bugle calls, 1–3 calls/bull). Bugle calls emitted in aggressive contexts exhibited ≥ 5 formants (F1 through F5) and no formants existed in bugle calls emitted in nonaggressive contexts.

	F1	F2	F3	F4	F5
Minimum (\bar{X})	1,147	1,692	2,224	3,016	3,801
SD	479	348	434	556	616
Maximum (\bar{X})	1,420	1,993	2,682	3,626	4,672
SD	474	237	573	642	677

be due to a physiological cause such as smaller body size and lung capacity or due to a functional cause such as the call not being used to advertise one’s location but to alert others to a specific situation. To our knowledge, no documentation exists that any female cervid other than North American elk emit vocalizations that are acoustically homologous to male breeding-season calls.

One of the few investigations determining that motivation–structural rules can apply to the acoustic structure of long-range vocalizations in mammals was Harrington’s (1987) study of howls of wolves (*Canis lupus*). The acoustic structure of wolf howls changed to include harsh, low-frequency sounds during aggressive interactions (Harrington 1987). Our study has revealed that motivation–structural rules also apply to the bugle calls of elk. As predicted by motivation–structural rules, bugle calls emitted in nonaggressive situations had whistle segments that were indeed “whistle-like,” tonal sounds, dominated by high frequencies. In contrast, bugle calls emitted in aggressive intrasexual contexts had whistle segments that were harsh, noisy sounds, dominated by low frequencies. This change in acoustic structure of the call may signal the willingness of an individual to engage in a fight, or the complexity of the call may convey information regarding the sender’s physical attributes, or both (Reby and McComb 2003).

Elk bugle calls emitted in aggressive contexts contained formants, whereas nonaggressive bugle calls lacked formants. Formants are sound peaks produced when signals resulting from laryngeal vocal fold vibrations pass through the supralaryngeal vocal tract (Fant 1960). In red deer roars, formant spacing, not pitch, appears to be an honest indicator of body size (Fitch 2000; Reby and McComb 2003; see also Riede and Fitch 1999). Red deer are capable of lowering their larynx while roaring, resulting in a longer vocal tract and lower formants (Fitch and Reby 2001). Our laboratory investigations of elk vocal tracts and field observations have revealed that elk also are able to move their larynx. However, examination of our data also has revealed that formants in elk bugles emitted in aggressive situations may vary with the context and degree of aggression, and we are currently investigating this hypothesis.

Our study has revealed that elk bugle calls have a complex structure and we have determined that motivation–structural rules (Morton 1977) can be applied to these long-range vocalizations. Studies are needed to elucidate how bugle call structure relates to individual physical characteristics and the

specific functions of the acoustic segments to understand the role of this complex vocalization in elk social behavior.

ACKNOWLEDGMENTS

We thank D. M. Armstrong, J. R. Watson, and J. Hanks for advice and guidance, and we thank K. R. and D. L. Johnson, M. S. Feighny, and S. P. and E. K. Mackessy for their constant support. We greatly appreciated the cooperation of the Rocky Mountain National Park staff, in particular T. Terrel and J. Visty, and the Rocky Mountain National Park Bugle Patrol. This project was supported in part by the University of Northern Colorado's School of Biological Sciences and Graduate Student Association and the Katie Edmonds Behavioral Ecology Laboratory. This work is dedicated to the life and memory of K. D. Johnson.

LITERATURE CITED

- AUGUST, P. V., AND J. G. T. ANDERSON. 1987. Mammal sounds and motivation—structural rules: a test of the hypothesis. *Journal of Mammalogy* 68:1–9.
- BOWYER, R. T., AND D. W. KITCHEN. 1987. Sex and age-class differences in vocalizations of Roosevelt elk during rut. *American Midland Naturalist* 118:225–235.
- CLUTTON-BROCK, T. H., AND S. D. ALBON. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69:145–170.
- CLUTTON-BROCK, T. H., S. D. ALBON, AND P. H. HARVEY. 1980. Antlers, body size and breeding group size in the Cervidae. *Nature* 285:565–567.
- CLUTTON-BROCK, T., F. GUINNESS, AND S. ALBON. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois.
- COMPTON, L. A., J. A. CLARKE, J. SEIDENSTICKER, AND D. R. INGRISANO. 2001. Acoustic characteristics of white-nosed coati vocalizations: a test of motivation—structural rules. *Journal of Mammalogy* 82:1054–1058.
- DARWIN, C. 1871. *The descent of man and selection in relation to sex*. Murray, London, United Kingdom.
- DE VOS, A., P. BROKX, AND V. GEIST. 1967. A review of social behavior of the North American cervids during the reproductive period. *American Midland Naturalist* 77:390–417.
- ESPMARK, Y. 1964. Rutting behaviour in reindeer (*Rangifer tarandus* L.). *Animal Behaviour* 12:159–163.
- FANT, G. 1960. *Acoustic theory of speech production*. Mouton and Company, The Hague, The Netherlands.
- FITCH, W. T. 2000. The evolution of speech: a comparative review. *Trends in Cognitive Science* 4:258–267.
- FITCH, W. T., AND D. REBY. 2001. The descended larynx is not uniquely human. *Proceedings of the Royal Society of London, B. Biological Sciences* 268:1669–1675.
- GEIST, V. 1982. Adaptive behavioral strategies. Pp. 219–278 in *Elk of North America: ecology and management* (J. W. Thomas and D. E. Toweill, eds.). Stackpole Books, Harrisburg, Pennsylvania.
- HARRINGTON, F. H. 1987. Aggressive howling in wolves. *Animal Behaviour* 35:7–12.
- HAUSER, M. D. 1996. *The evolution of communication*. Massachusetts Institute of Technology Press, Cambridge.
- KILEY, M. 1972. The vocalizations of ungulates, their causation and function. *Zeitschrift für Tierpsychologie* 31:171–222.
- MARLER, P. 1967. Animal communication signals. *Science* 157:769–774.
- MCCOMB, K. 1987. Roaring by red deer stags advances the date of oestrus in hinds. *Nature* 330:648–649.
- MCCOMB, K. 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behaviour* 41:79–88.
- MITANI, J. C. 1985. Sexual selection and adult male orangutan long calls. *Animal Behaviour* 33:272–283.
- MORTON, E. S. 1977. On the occurrence and significance of motivation—structural rules in some bird and mammal sounds. *American Naturalist* 111:855–869.
- MORTON, E. S. 1982. Grading, discreteness, redundancy, and motivation—structural rules. Pp. 183–212 in *Acoustic communication in birds* (D. Kroodsma and E. H. Miller, eds.). Academic Press, New York.
- MURIE, O. J. 1932. Elk calls. *Journal of Mammalogy* 13:331–336.
- MURIE, O. J. 1951. *The elk of North America*. Stackpole Books, Harrisburg, Pennsylvania.
- REBY, D., M. IZQUIERDO, A. J. M. HEWISON, AND D. PEPIN. 2001. Red deer (*Cervus elaphus*) hinds discriminate between the roars of their current harem holder stag and those of neighbouring stags. *Ethology* 107:951–959.
- REBY, D., AND K. MCCOMB. 2003. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour* 65:519–530.
- RIEDE, T., AND W. T. FITCH. 1999. Vocal tract length and acoustics of vocalization in the domestic dog *Canis familiaris*. *Journal of Experimental Biology* 202:2859–2867.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. 3rd ed. W. H. Freeman, New York.
- STRUHSAKER, T. 1967. Behaviour of elk (*Cervus canadensis*) during the rut. *Zeitschrift für Tierpsychologie* 24:80–114.

Submitted 21 March 2006. Accepted 24 March 2006.

Associate Editor was Floyd W. Weckerly.