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Sex and Age-class Differences in Vocalizations of Roosevelt Elk During Rut

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ABSTRACT: Vocalizations of free-ranging Roosevelt elk (*Cervus elaphus roosevelti*) were studied at Gold Bluffs Beach, Prairie Creek Redwoods State Park, Humboldt Co., California, from August through November 1973. Significant differences were found in types and rates of elk vocalizations among different sex and age classes. Bull vocalizations varied with age and social status. Sonograph analyses revealed structural similarities in elk cohesion calls, bugles and yelps; bugles and yelps may be elaborations of cohesion calls. Bugling and yelping by master bulls occurred primarily in male-female encounters and may have functioned to bring cows closer together; bulls bugled most often when the harem was widely dispersed. Bulls vocalized less frequently in aggressive interactions between bulls where bugling and yelping clearly were related to male dominance.

INTRODUCTION

Despite extensive literature concerning mammalian vocalizations (Marler, 1955, 1967; Collias, 1960; Sebeok, 1968; Tembrock, 1968), comparatively little information exists for ungulates. Much of the recent literature on ungulate vocalizations was summarized by Kiley (1972), but quantitative descriptions of vocalizations and data on their causation were presented primarily for domestic species. Further, quantitative research on wild species often has focused on alarm vocalizations (Hirth and McCullough, 1977; Yahner, 1980; Richardson *et al.*, 1983) or calls between mother and young (Espmark, 1971, 1975).

Types and variability of vocalizations in other subspecies of *Cervus elaphus* have been well-documented (Murie, 1932, 1951; Darling, 1937; Johnson, 1951; Ahlen, 1965; Bubenik and Brna, 1967; Harper *et al.*, 1967; Struhsaker, 1967; Olsen, 1979), and Peters (1980) reviewed the vocalizations of North American elk. Data on vocalizations of Roosevelt elk (*C. e. roosevelti*), however, were limited to qualitative descriptions (Graf, 1955; Harper *et al.*, 1967), and information on the function and circumstances under which these sounds occurred was lacking. Further, Clutton-Brock and Albon (1979) noted that roaring by red deer (*C. e. scoticus*) stags occurred primarily during aggressive interactions between males, but roaring also was directed toward females in the stag's harem, suggesting a male-female function for this vocalization. Miura (1984) also noted that bugle-like "moans" of male sika (*Cervus nippon*) were given in response to the activities of females. The purpose of this study was to quantify sex and age-class differences in vocalizations from a free-ranging population of Roosevelt elk during rut, and to examine the behavioral context in which vocalizations occurred.

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STUDY AREA

Research was conducted during 1973 on Gold Bluffs Beach, Prairie Creek Redwoods State Park, Humboldt County, California (41°23'N, 124°06'W). Gold Bluffs Beach is a long (6 km), narrow (0.1-0.5 km) stretch of coastal prairie separated from redwood (*Sequoia sempervirens*) forest by steep cliffs. The prairie is interspersed with red alder (*Alnus rubra*) groves that surround numerous creeks along the beach. Gold Bluffs Beach possesses a mild climate characterized by early morning and late evening fogs. More complete descriptions of the study area are available elsewhere (Harper *et al.*, 1967; Franklin *et al.*, 1975; Bowyer, 1981).

The Gold Bluffs Beach elk herd was composed of four master bulls (bulls that held a harem during rut), six bachelor bulls, three yearling bulls, 19 cows (including two female yearlings), and seven calves. All bulls were recognizable as individuals but, with the exception of two cows with ear tags, individuals in other sex and age classes were not recognized consistently.

METHODS

Results are based primarily upon 311 hr of direct observation of elk during their mating season (August-November). Observations were made from 0700-0200 Pacific Standard Time with the unaided eye or 7 x 26 binoculars over distances of 5-100 m. Most observations were made from a vehicle to minimize disturbance to elk.

Focal-group sampling and an all-occurrences log (Altmann, 1974) were used to quantify frequency of vocalizations. Nomenclature for vocalizations follows Murie (1951) and Struhsaker (1967). Every discrete sound emitted by an elk was scored as a separate vocalization. Sex, age class, body posture and associated behaviors were noted for each caller, as well as sex and age classes of interacting elk. Vocalizations were sampled only when elk were observed calling, and these acts could be assigned to an individual or sex and age class. Further, if the behavioral context of a vocalization was in doubt, the vocalization was classified as "undetermined." Elk were considered to vocalize toward another individual if they were facing within 45° of each other (Clutton-Brock and Albon, 1979). Additionally, locations of elk were plotted on an aerial photograph at 10-min intervals, and the greatest distance across the herd was estimated.

Vocalizations were analyzed on an acts-per-active hour (A/AH) basis that provided an average rate of vocalizing for individuals in each sex and age class (Bowyer, 1981). Acts per active hour were selected over total hours of observation because different sex and age classes of elk were observed for varying time intervals, and each exhibited different patterns of activity (Bowyer, 1981). Only one of 2013 vocalizations was emitted by an inactive (bedded) individual. A parabolic microphone and a Sony TC800B tape recorder were used to record vocalizations that were analyzed later with a K-Electric 6061A Sona-Graph.

The *G*-test of independence (Sokal and Rohlf, 1969:591) was used to compare elk vocalizations; expected values were determined by calculating the number of times a vocalization would have occurred if sex and age classes vocalized at the same rate. The Spearman rank correlation (Siegel, 1956) was employed to examine the relationship between percent of bugling and distance across the harem, and the *G*-test for goodness of fit (Sokal and Rohlf, 1969:563) was used to test for differences in harem dispersion when bulls bugled, and during 10-min-interval scans (Altmann, 1974) when they did not do so.

RESULTS

DESCRIPTIONS AND BEHAVIORAL CONTEXTS OF ELK VOCALIZATIONS

Cohesion call.—Elk typically emitted cohesion calls from an alert posture (head held high and horizontal, ears up and forward, nostrils flared, tail not raised). This call consisted of a short, high-pitched bleat of moderate volume and frequency (Fig. 1). The vocalization often was repeated several times with a short interval between calls. Cows and

calves often gave cohesion calls prior to nursing; 41% of 932 cow cohesion calls occurred immediately prior to 125 nursing bouts ($\bar{X}$ = 3.1 cow vocalizations per bout). A significantly ($P<0.001$) smaller proportion (22% of 446) of calf cohesion calls were associated with nursing ($\bar{X}$ = 0.8 vocalizations per bout). It was our impression that calf cohesion calls were evoked by cohesion calls from cows. Cohesion calls by master bulls also followed cohesion calls by other elk, again suggesting that they were elicited by these vocalizations.

Associated behaviors suggested that cohesion calls facilitate elk in locating one another. On two occasions, master bulls emitted a series of cohesion calls when a cow moved a short distance from the harem. In addition, yearling bulls exchanged cohesion calls with cows when they were driven from the harem by the master bull.

Alarm squeal.—The body conformation of elk giving alarm squeals was characteristic of "alarmed" elk (head held high with muzzles tilted upward, ears pointing slightly backward, tail erect, running or trotting away from the disturbance). Alarm squeals were prolonged, high-pitched bleats. Cows gave a different alarm vocalization, the alarm bark (*see* Struhsaker, 1967, for sonograph) in June, but never during rut. Alarm squeals were given only by yearling bulls in response to the charge of master bulls attempting to drive yearlings from their harems. The peak of alarm squeals by yearlings in September (Fig. 2) coincided with vigorous rutting behavior by master bulls during that period.

Hiss.—Hissing occurred during low-stretch (broad-side display) postures. The sides of a bull's upper lip were lifted and canine teeth were exposed during this display. Tooth-

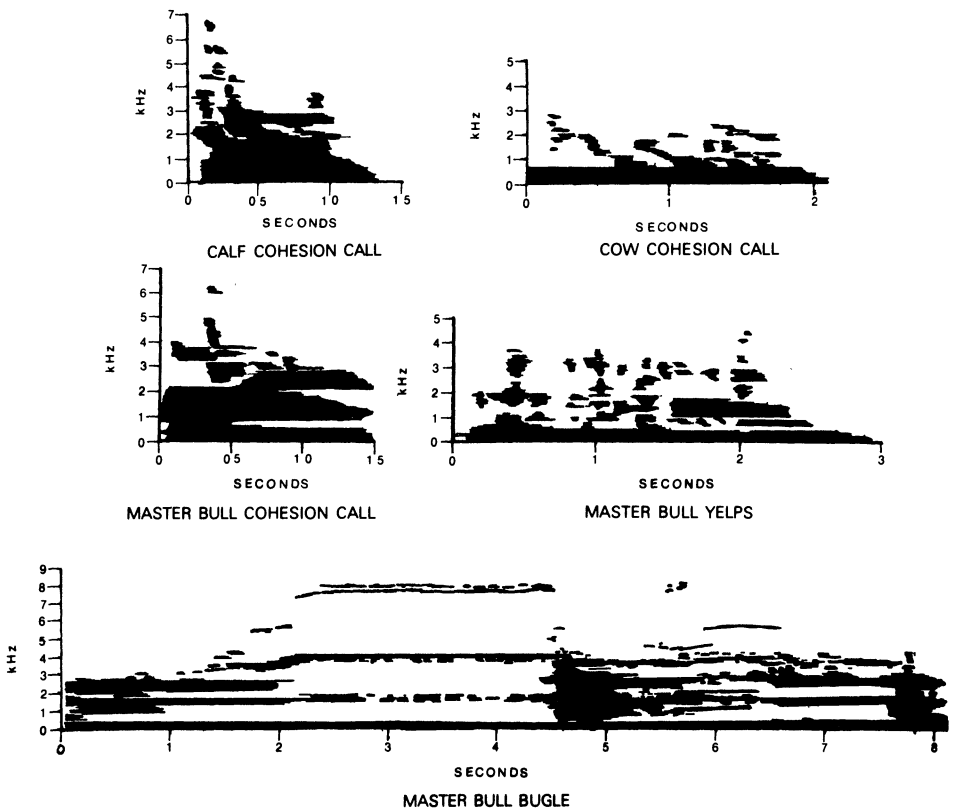

Fig. 1.—Sonographs of Roosevelt elk vocalizations during rut recorded at Gold Bluffs Beach, Prairie Creek Redwoods State Park, Humboldt County, California

grinding occasionally accompanied hissing. Hissing was audible over comparatively short distances (≤ 20 m) and accompanied all low-stretches in which we were close enough to detect the sound. Hissing occurred throughout the year in dominance interactions involving both master and bachelor bulls. Yearling bulls and cows were not heard to hiss or observed to display low-stretch (broad-side) postures with which hissing was linked in other age classes of males.

Sparring squeaks.—Sparring squeaks were a continuous sequence of high-pitched, low-volume bleats emitted during mock fights between bulls (*see* Olsen, 1979, for sonograph). Sparring squeaks were emitted only by bachelor bulls and accompanied all 26 sparring bouts (ritualized fights) between these males. Twice near the end of rut, a master bull sparred with a bachelor bull. During these interactions, only the bachelor bull vocalized, and the rapidity and volume of sparring squeaks increased as the master bull drove the bachelor bull backward.

Bugle.—A bugling bull stretched his neck outward, tipped his antlers back over the body, raised his muzzle slightly, directed his ears backwards, and opened his mouth (Fig. 3). Bugles were initiated with a high-pitched whistling sound and terminated in a low moan. Bugles had the longest duration and highest volume and frequency of all vocalizations (Fig. 1), but audibility was poor at >100 m. This poor audibility may have

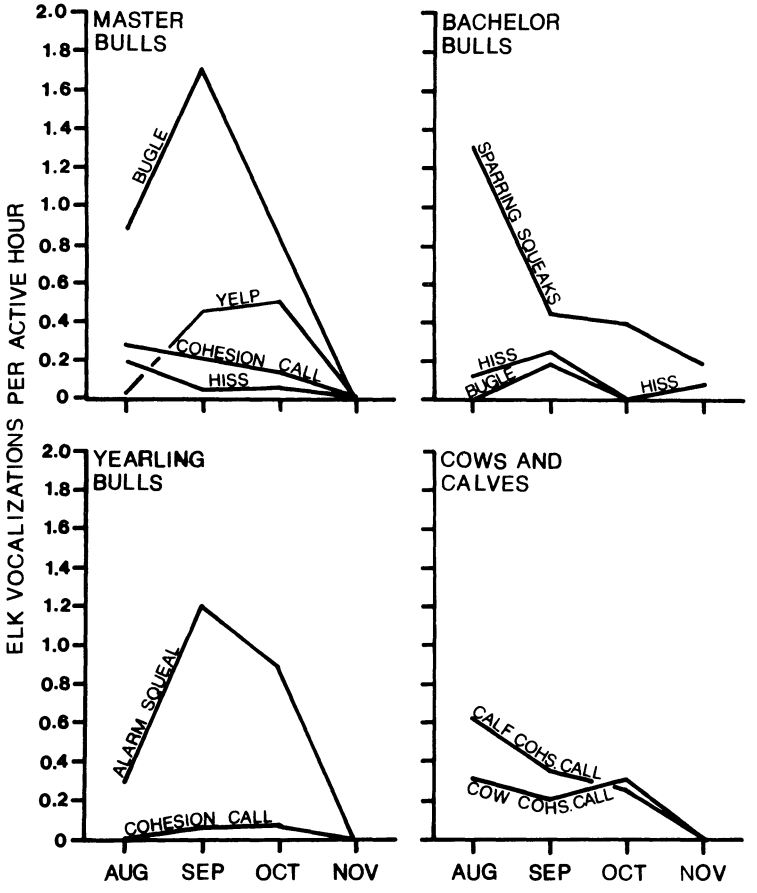

Fig. 2.—Monthly rates (A/AH) of vocalizations for sex and age classes of Roosevelt elk at Gold Bluffs Beach, Prairie Creek Redwoods State Park, Humboldt County, California

been due to foggy conditions and the noise from nearby surf, and is in strong contrast to our experience with louder bugles of Rocky Mountain elk (*Cervus elaphus nelsoni*).

Bugling by master bulls occurred in both male-male and male-female interactions (Table 1). In most cases, we distinguished bugles directed at bulls from those apparently intended for cows. When potential opponents seeking possession of the harem were encountered, master bulls trotted away from the harem in an alert posture while staring directly at the intruding bull. The master bull then assumed a bugling posture and began vocalizing. The approach of a bugling harem master caused 37 of 39 intruding bulls to take flight. In two cases, however, bulls appeared more evenly matched and exchanged bugles as they approached one another. Bugling preceded both serious fights over the possession of cows. When attacking yearling bulls in the harem, the master bull bugled immediately before or after chasing them away from cows (Table 1).

Bugles directed toward cows occurred while the master bull herded the harem (Fig. 3). In these instances, no bulls were visible or in the immediate vicinity (≤ 100 m) of the harem. On 10 occasions in which the master bull directed bugles toward cows with-

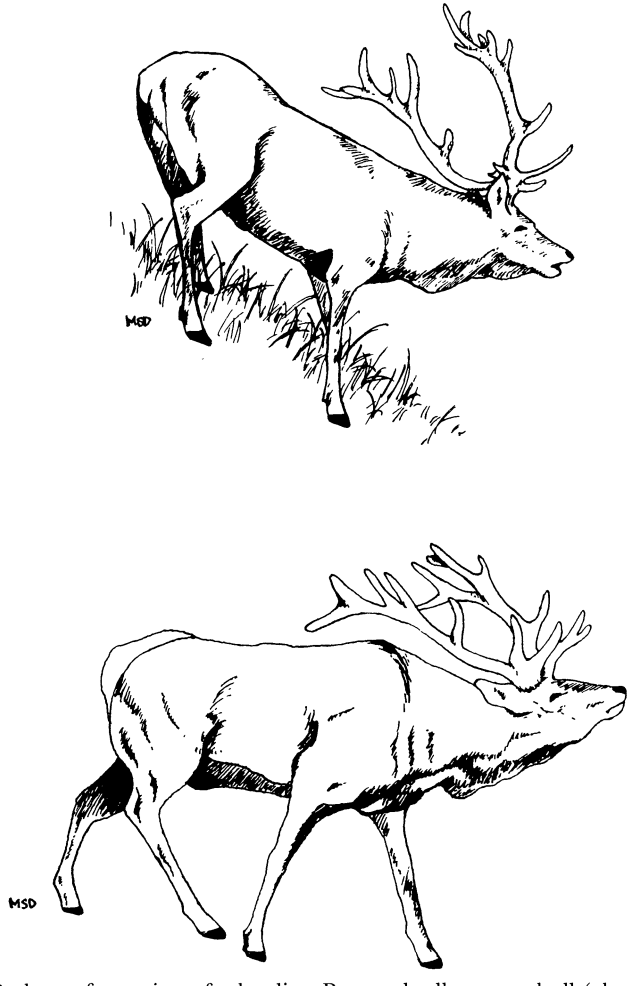

Fig. 3. — Body conformation of a bugling Roosevelt elk master bull (above), and of a herding posture (broad-side display) (below)

out herding them, cows ran toward and gathered around the bull. Master bulls bugled significantly ($P<0.001$) more often while herding cows than when interacting with bulls (Table 1). Bugling increased significantly ($r_s = 1.00$, $P<0.01$) as the harem became more dispersed. The *G*-test for goodness of fit showed these values differed significantly ($P<0.001$) from those expected from the greatest distance across the herd (Fig. 4).

Master bulls bugled at a rate 61 times greater than bachelor bulls (Table 2, Fig. 2). The primary master bull averaged 1.65 bugles per active hour; this was considerably greater than for secondary and tertiary master bulls (0.14 bugles per active hr) that acquired harems late in the mating season.

Yelp.—The posture of a yelping bull was similar to that described for bugling, but the antlers were tipped farther over the back. Yelping commonly was accompanied by contractions of the penile region with simultaneous emission of short spurts of urine, and usually occurred as the bull walked or trotted in a stiff-legged gait. Yelps were of moderate volume and frequency, and consisted of a series of 3-7 similar elements (Fig. 1). Yelps were emitted only by master bulls and occurred only during the mating season. Yelps occurred significantly ($P<0.01$) more often in male-female than male-male interactions (Table 2). This vocalization typically was directed toward other elk in close proximity (≤ 20 m) and occurred when the bull appeared "excited," especially when he vigorously herded cows or charged bulls. Yelps and their accompanying body posture attracted the immediate attention of nearby individuals. Yelps were given immediately after bugles on three occasions.

SEX AND AGE-CLASS DIFFERENCES IN ELK VOCALIZATIONS

Elk were heard vocalizing on 2013 occasions during rut. Cows and calves gave only cohesion calls, yearling bulls primarily emitted alarm squeals, bachelor bulls emphasized sparring squeaks, and master bull vocalizations were dominated by bugles and yelps (Table 1).

Significant differences ($P<0.05$) occurred in the frequency with which all sex and age classes of elk emitted the different vocalizations (Table 1). Except for the cow-calf pairing, significant differences ($P<0.02$) were found between all sex and age class pairings for the frequency of cohesion calls. Significant differences ($P<0.001$) in the frequency with which alarm squeals were emitted were found only for pairings involving yearling bulls. Bachelor bulls differed significantly ($P<0.001$) from all other sex and age classes in the frequency with which they emitted sparring squeaks. Significant differences in the frequency of hissing were found for pairings with bachelor bulls ($P<0.05$) and master bulls ($P<0.02$), but not between them ($P>0.20$). Differences in the frequency with which bugling occurred were found only for pairings with master bulls ($P<0.001$); this pattern also held for yelping and pairings with master bulls ($P<0.001$). Master bulls had greater diversity of vocalizations than other sex and age classes (Table 2).

Bugling and yelping were most frequent at the height of rut in September and October; alarm squeals by yearling bulls also were highest during this period (Fig. 2). Mas-

TABLE 1.—Behavioral contexts in which master bulls emitted bugles and yelps during rut, Gold Bluffs Beach, Prairie Creek Redwoods State Park, Humboldt Co., California, 1973

Vocalization	Herding cows		Challenging master and bachelor bulls		Challenging yearling bulls		Charging yearling bulls		Undetermined	
	N	%	N	%	N	%	N	%	N	%
Bugle	94	45	25	12	14	7	0	0	77	36
Yelp	44	62	1	1	0	0	15	21	11	16
Total	138	49	26	9	14	5	15	6	88	31

ter bulls were observed copulating with cows twice in mid-September (Bowyer, 1976). Sparring squeaks by bachelor bulls and cohesion calls by other sex and age classes declined as rut progressed (Fig. 2).

Differences in frequency and type of vocalizations occurred for various sex and age classes of Roosevelt elk. Additionally, male elk altered their use of vocalization pattern with respect to their age and social status (Table 1).

DISCUSSION

FUNCTIONS OF ROOSEVELT ELK VOCALIZATIONS

Cohesion call.—The behavioral context in which Roosevelt elk cohesion calls occurred strongly suggests that they facilitate elk in locating one another and probably function to draw them together. Kiley (1972) noted that contact calls in ungulates typically were short, low-frequency vocalizations that often were repeated; this was the case for Roosevelt elk cohesion calls. Johnson (1951) located Rocky Mountain elk (*Cervus elaphus nelsoni*) calves by imitating a calf cohesion call that induced cows to return to the hiding place of their calves. Cohesion calls among Roosevelt elk not associated with nursing occurred when cows and calves were separated; this lends further support to our interpretation of this vocalization.

Alarm squeal.—Murie (1932) reported that frightened Rocky Mountain elk calves modified the cohesion call into a prolonged scream that attracted their dams. Alarm squeals of Roosevelt elk yearling bulls probably were similar modifications of cohesion calls.

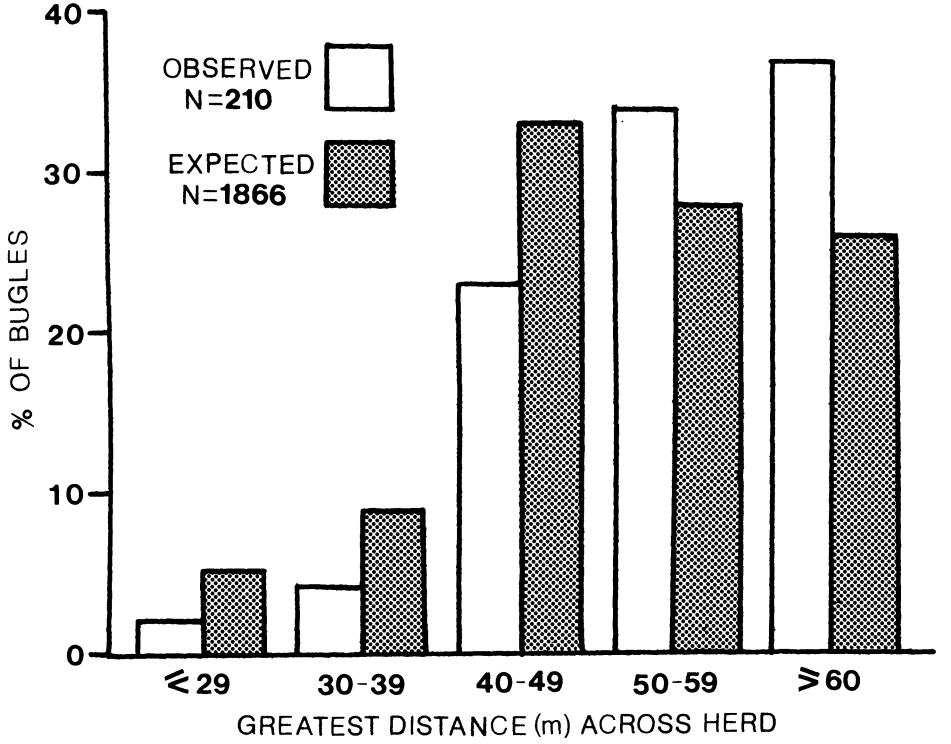

Fig. 4.—Percent of 210 bugles emitted by Roosevelt elk master bulls relative to the maximum distance across the harem, Gold Bluffs Beach, Prairie Creek Redwoods State Park, Humboldt County, California. Expected values for the goodness of fit test were generated from the proportions of scan-samples in each of the distance categories

TABLE 2.—Summary of types and rates of vocalizations emitted by Roosevelt elk during rut, Gold Bluffs Beach, Prairie Creek Redwoods State Park, Humboldt Co., California, 1973. N = number of times vocalizations heard; A/AH = acts per active hour

	Cohesion call			Alarm squeal			Sparring squeaks			Hiss			Bugle			Yelp			Active elk hr	Mean No. elk observed per hr
	N	A/AH	%	N	A/AH	%	N	A/AH	%	N	A/AH	%	N	A/AH	%	N	A/AH	%		
Calves	446	0.40	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	171	6.5
Cows	932	0.28	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	182	18.4
Yearling Bulls	14	0.04	5.5	240	0.76	94.5	0	0	0	0	0	0	0	0	0	0	0	0	153	2.1
Bachelor Bulls	0	0	0	0	0	0	46	0.85	88.5	5	0.09	9.6	1	0.02	1.9	0	0	0	16	3.4
Master Bulls	34	0.20	10.3	0	0	0	0	0	0	14	0.08	4.3	210	1.22	63.8	71	0.41	21.6	172	1.0

Sparring squeaks.—Sparring squeaks likely functioned as appeasement to reduce aggression during sparring. The association of these vocalizations with sparring among bachelor bulls, and the increasing volume and rate of delivery of this vocalization by subordinate bachelor bulls during sparring bouts with dominant master bulls support this interpretation.

Hiss.—Kiley (1972) noted that hisses and growls often accompanied aggressive interactions in ungulates. Aggressive postures and behaviors associated with hissing by Roosevelt elk bulls support this observation. It is likely that hisses were used as threats between male elk.

Bugle.—Several ideas have been forwarded to explain the functional significance of bugling. Numerous authors (Darling, 1937; Murie, 1951; Struhsaker, 1967; McCullough, 1969; Butzler, 1974) noted that *Cervus elaphus* exchanged bugle-like vocalizations in an aggressive context. These sounds may express dominance and allow assessment of the fighting ability of males (Clutton-Brock and Albon, 1979). This held for bugling by Roosevelt elk master bulls; this vocalization preceded all serious fights between bulls. Nonetheless, bugling by Roosevelt elk occurred more frequently during male-female interactions.

The body posture of a bugling bull resembles that of a bull herding a harem (Fig. 2). Similar postures occur in other cervids during sexual approaches toward females, and among most cervids, including elk, in aggressive interactions between males (Geist, 1966; DeVos *et al.*, 1967). Thus, these dominance displays serve both in the courtship of females and in aggression between males. The body conformation of a courting bull elk, however, is the antithesis of that exhibited when herding cows or bugling (Geist, 1966; Struhsaker, 1967; McCullough, 1969; Bowyer, 1976). We suggest the differences between elk and other cervid species relates to the harem mating system of elk and the use of the herding posture in keeping females close together. Herding is a highly aggressive display. Master bulls commonly direct antler threats toward cows and occasionally strike them with their antlers (Bowyer, 1976). Bulls neither assumed the aggressive body posture associated with bugling when courting cows nor bugled during these sexual approaches. Thus, bugling by master bulls probably is not sexual in nature. Bugling, however, might attract potential mates. Home ranges of Roosevelt elk cow-calf herds were widely dispersed (Mandel and Kitchen, 1979) and the composition of the Gold Bluffs Beach herd was highly stable throughout rut (Bowyer, 1976). We did not observe bulls add new cows to harems by bugling; this was accomplished through combat with other bulls (Bowyer, 1976). Thus, Roosevelt elk bulls bugled frequently in situations that were unlikely to attract additional mates. Both Rocky Mountain elk (Struhsaker, 1967) and tule elk (McCullough, 1969) have a greater potential to attract females by bugling; female groups are more labile and less dispersed, and bugles of these subspecies are audible over far greater distances than those we heard for Roosevelt elk.

If bugles were sexual in nature, they should be associated with sexual behaviors, but were not for Roosevelt elk. Bugling might inadvertently attract rival males, but if this vocalization served primarily as a sexual attractant, the clear use of this display in male-male dominance interactions is difficult to explain.

It is plausible the bugle draws the attention of cows to the herding-like posture of a bugling bull; herding bulls directed many of these vocalizations toward the harem. Thus, we hypothesize a bugle communicates the bull's intention to bring harem members closer together. Supporting this contention are the observations that cows occasionally ran toward the bull after he bugled, that bulls bugled more frequently when the harem was widely dispersed (Fig. 4), and that a significantly higher percent of bugles were associated with interactions involving solely cows (Table 2). Unfortunately, it was difficult to distinguish between the influence of bugling and the herding activities of master bulls on the response of cows to these behaviors because bugling and herding were linked in most interactions involving cows. The strong association of these behaviors, however, provides additional support for our hypothesis. Roosevelt elk bachelor bulls at-

tempted to steal cows from the harem as it became dispersed (Bowyer, 1976), and Clutton-Brock *et al.* (1979) noted similar behavior for red deer. We hypothesize that bugling is important in keeping the harem tightly grouped and, hence, reducing theft of cows by other bulls.

A comparison of sonographs reveals a striking resemblance across frequencies between cohesion calls and those portions of the bugle between 4.5 - 5.5 seconds and 7.5 - 8.0 seconds (Fig. 1). Structural similarities between these vocalizations suggest the bugle may be an elaboration of the cohesion call. Consequently, the bugle may have the analogous function of a cohesion call in bringing elk cows together. The use of the bugle primarily while herding cows (Table 2) supports this interpretation. Structural similarities between cohesion calls and bugling also occur in the vocalizations of Rocky Mountain elk (Struhsaker, 1967; Olsen, 1979).

Bugling during aggressive encounters between bulls may have developed from the occurrence of these vocalizations in a male-female context. Two bulls vocalizing to draw the attention of cows to their herding postures undoubtedly would become aware of one another. Because the herding posture strongly resembles the broad-side display associated with aggression between bulls (DeVos *et al.*, 1967; Geist, 1966), it is logical that bugles might acquire the secondary role of a challenge or threat among bulls.

Yelp.—The association of yelping with a herding posture by master bulls (Fig. 2), and the use of this vocalization primarily in a male-female context (Table 2), suggests yelping may be functionally similar to bugling. Indeed, these two vocalizations often occurred together in Rocky Mountain elk (Struhsaker, 1967). Marler (1955) noted that sudden changes in frequency and volume of a vocalization enhanced the opportunity for binaural comparisons, and hence, increased the ease with which the animal emitting the sound could be located. Conversely, vocalizations of higher frequency and volume would carry over greater distance, but would be more difficult to locate (Marler, 1955). Yelps by master bulls obtained the immediate attention of nearby elk, whereas the acoustic properties of the bugle made it more suitable for communication over greater distances. Thus, the causation and function of bugles and yelps may be similar, the major differences relating to the distance over which the vocalization travels.

Clutton-Brock and Albon (1979) demonstrated the role of roaring in the aggressiveness and dominance of male red deer, but their work also suggested that this vocalization was involved in the stag's control of harem dispersion. Some bugle-like vocalizations of male sika also were directed toward females (Miura, 1984). We suggest that control of the harem is a major function of Roosevelt elk bugling and yelping, and that these vocalizations also may possess a similar function in other subspecies of *Cervus elaphus*.

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