THE MOOSE BELL: A VISUAL OR OLFACTORY COMMUNICATOR?

Dale G. Miquelle[1] and Victor Van Ballenberghe
Institute of Northern Forestry
308 Tanana Drive
Fairbanks, AK 99701

ABSTRACT: Two current hypotheses that explain the evolutionary significance of the moose (Alces alces) bell are: 1) during the rut the male bell disseminates and transfers by contact, the urine of the bull close to or directly onto the cow, and; 2) the bell acts as a visual cue that relates to sex and age, which in turn may be associated with rank. We tested the first hypothesis by describing wallowing behavior, and determining whether females initiated contact with bulls' bells more than expected by chance. The second hypothesis was tested by comparing bell morphology in two populations of moose, and by relating the outcome of agonistic interactions to bell shape. Observations on wallowing behavior supported the hypothesis that the bell acts as a carrier of olfactory cues. However, females make physical contact with male bells less than expected by chance. Populations in Alaska and Ontario had similar age- and sex-related variations in bell shape. No relationship was found between bell morphology and dominance among females or among males during the antlerless period. We hypothesize that bell shape is a secondary sexual characteristic most important during the rut, and that moose may use bell morphology to assess social status of conspecifics.

ALCES 21 (1985)

---

[1] Present address: Department of Wildlife Resources, University of Idaho, Moscow, ID 83843

Although the bell is a prominent anatomical feature of moose, it has rarely been the subject of study. Timmermann (1979) and Timmerman et al. (1985) have made morphometric measurements of the bell, investigated its development, histology, and vascularization, and have speculated about its function. Hypotheses for the evolutionary significance of the bell abound (see Timmerman 1979). Specialized structures of the neck and throat region are fairly common in ungulates, taking the form of manes, beards, and skin appendages (Timmermann 1979). None of these anatomical features have any known physiological function. Because displays and behavioral interactions between ungulates are largely directed towards and emanate from the head region (Walther 1977, 1984, Klingel 1977), it is generally believed that structures such as bells are social organs that play a role in intraspecific communication.

Currently, two hypotheses exist to explain the evolutionary significance of the moose bell. The first proposes that the male bell disseminates and transfers by direct contact with a cow, the urinary and possibly salivary pheromones of the bull close to or directly onto the cow during the rut (Bubenik 1983). The hypothesis states that the bull's bell is soaked in urine during wallowing behavior, and that scent is transferred to the cow's bell in 3 ways: 1) cows actively seek out bulls, and rub their facial region on the bull's bell, 2) cows rub their bells in pits which have been urine-soaked by bulls; and 3) cows make direct nasal contact while a male urinates. The saturated cow bell then acts as a scent disperser that stimulates ovulation. Supporting evidence for this hypothesis comes from the observations that: 1) cows have been seen to rub their heads on bull's bells and are strongly attracted to male urine (Bubenik 1983, pers. obs.), and; 2) scent-urination is common in ungulates

(Coblentz 1976), and males of some ungulate species, including Gray's waterbuck (Onotragus megaceros) and species of Capra, urinate directly onto the beard or neck region (Shank 1972, Walther 1984), while other males, such as red deer and wapiti (Cervus elaphus) smear the neck with urine while wallowing (Geist 1982).

The second hypothesis proposes that the bell evolved primarily as a visual cue, and that size and shape of bells may be secondary indicators of sex and relative age, especially during the antlerless period (Timmermann 1979). Because social rank among males of polygynous ungulate species is often age-related (Geist 1971, Clutton-Brock et al. 1979), bell shape may act as a visual display of rank. The presence of antlers or horns on other ungulates appears sufficient for differentiation of sexes, and may be important in assessment of dominance (Geist 1966, 1971, Bartos and Hyanek 1983, Bubenik 1983). However, secondary sexual characteristics are common: male cervids, including bull caribou (Rangifer tarandus) and wapiti have manes; Caprini such as urial (Ovis orientalis), barbary sheep (Ammontragus lervia), goats (Capra spp.), and Rocky Mountain goats (Oreamnos americanus) have beards and neck ruffs; bovids such as bison (Bison bison), gaur (Bos gaurus), eland (Taurotragus spp.) and nilgai (Boselaphus tragocamelus) carry beards and skin appendages. Beard size does vary with age in some species of sheep (Lyddekker 1913, in Geist 1971), and beard and dewlap size is sexually dimorphic in bison and gaur (Lott 1974, 1979, Schaller 1967).

We tested the first hypothesis by assuming that: 1) if the moose bell evolved primarily to be an organ used during the rut to disperse the scent of urine to cows from either the male or female bell by airborn and direct physical contact, both bulls and cows should expend considerable energy

soaking the bell with urine, and; 2) if cows are attracted to a bull's bell in an attempt to investigate chemical cues or impregnate themselves with the scent, cows should make more physical contact with the bell than with other parts of a bull's body. To examine these assumptions, we described the wallowing behavior of bulls and cows and compared the observed frequencies of female contact with various parts of a bull's body to those expected by chance.

To test the second hypothesis, we compared our observations on bell morphology of A. a. gigas in Denali National Park to observations by Timmermann et al. (1985) of A. a. in the overlap zone between A. a. andersoni and A. a. americana in Ontario (Peterson 1955). Consistency between populations with regard to age- and sex-related bell morphology would support the hypothesis that bell shape acts as a visual cue of social status. To test whether bell morphology is correlated with rank, we analyzed male-male, female-female, and male-female agonistic interactions to see if dominant animals carried certain bell shapes more frequently than expected by chance. Because presence or absence of antlers, and antler size are likely the most important visual signals of sex and rank (Geist 1966, 1971, Bubenik 1983, Bartos and Hyanek 1983), we separated interactions into 2 periods: 1) autumn (antlered period); and 2) winter/spring (antlerless/early growth periods).

METHODS

All observations were made in Denali National Park, Alaska. Data on wallowing behavior and male-female contact were collected from September 1 to October 10, 1981-1984. Data on bell morphology and agonistic behavior were collected from May to October, 1982, 1983 and 1984, and January through April, 1985.

Bulls were assigned to one of 5 antler classes based primarily on antler spread, but also on body size (for yearlings), and number of tines (both antlers combined): class 1 = yearling, class 2 = 76-102 cm (30-40 inches) antler spread, class 3 = 103-127 cm (41-50 inches), class 4 = 128-152 cm (51-60 inches), and class 5 = greater than 152 cm (60 inches). These classifications were based on our visual assessment of antler size, and accuracy was supported in 2 ways. On the 11 occasions when bulls with fully developed antlers were immobilized, actual spread measurements lay within our estimated size classes 9 times. There was also a correlation between number of tines and antler class (Spearman's RHO = 0.88, $P < 0.01$, $N = 53$); there were significant differences in the median number of tines of all antler classes (Mann Whitney U-tests, $P < 0.05$) except classes 3 and 4.

Bell morphology was described through direct observations, and the use of photographs. Bells of cows and bulls were assigned to one of 8 classes, based on relative size and shape (Figure 1). Bell types are based largely on figures by Timmermann (1979) and Timmermann et al. (1985). Known individuals were assigned to new bell classes on a yearly basis.

Female body contact with males occurred when cows approached bulls and made nasal contact (apparently while smelling) or rubbed parts of their bodies on some part of the male. The area of the male's body that females contacted was recorded as: 1) nose; 2) neck, bell and chest region; 3) antlers, 4) body from shoulders to rear, and; 5) genital region. If a female made contact with more than one area, each was recorded as a separate occurrence.

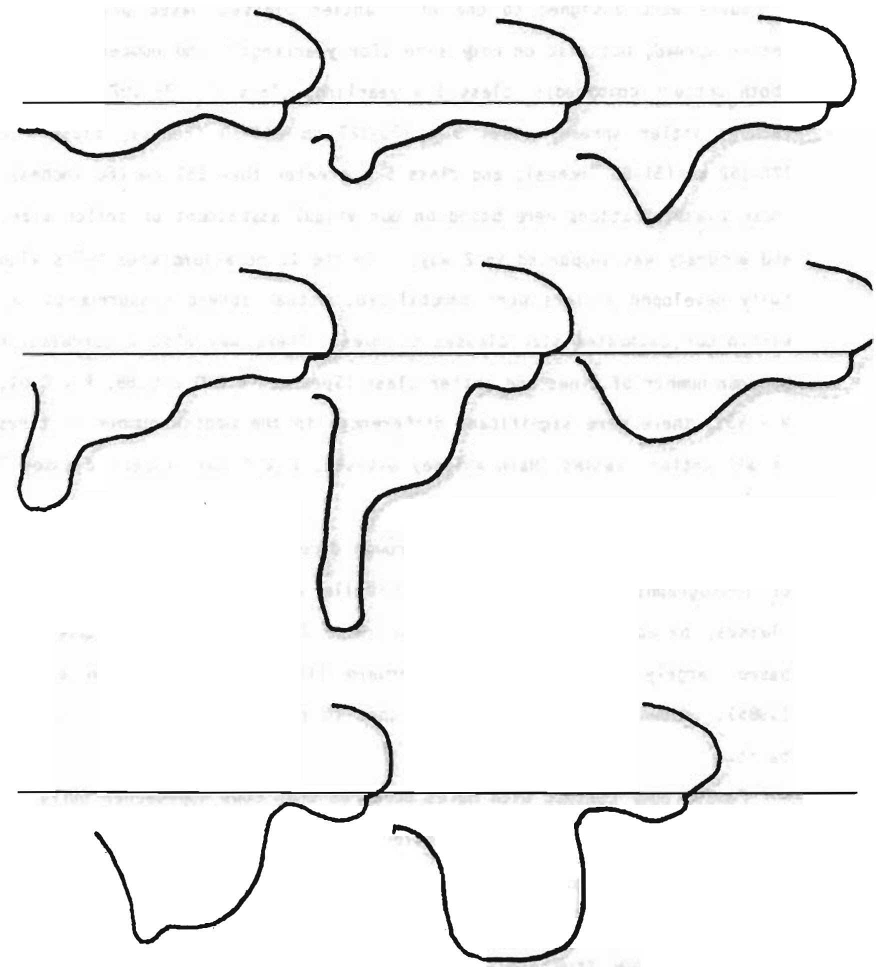

FIGURE 1. Eight typical shapes used to classify bell morphology of moose, after Timmerman (1979).

The bell shape of animals involved in dyadic agonistic interactions was noted. Agonistic behaviors included: head-high display, front leg kicking, flailing (Geist 1963, Walther 1984), antler threat (Walther 1984), rush threat, parallel walk, and fighting (Clutton-Brock et al. 1983, Walther 1964, Peek et al. submitted). In agonistic encounters the submissive animal was defined as that individual who first retreated from the interaction. Interactions were considered distinct if they were separated by at least one minute of no occurrence of an agonistic act.

Interactions between females were observed throughout the year. Observations of male-male and male-female interactions during the antlerless/early stages of antler growth period were made from Jan. 1 to June 15. Observations on interactions between males during the antlered period (August 25 to October 10) are based on data from Peek et al. (submitted). Associations between antler size and bell class, and between bell shape and dominance were tested with chi-square analyses. Differences were considered significant when $P < 0.05$.

RESULTS

Wallowing

Bulls dug and urinated in pits on 30 occasions during which we recorded the full sequence of behavior. On 18 occasions (60%), bulls splashed urine with their front hooves while their heads were lowered close to the ground and angled slightly to the side, as described by Bubenik (1983). With the head down, urine was splashed onto the antlers, head, bell, and neck. Wallowing behavior usually involved lying in the pit, with head up (normal bedded posture), with occasional agitated movements: there was seldom an attempt to get the neck or bell directly

in the pit. Wallowing was seen 13 times (43%) after pit digging and urination. Splashing, if it occurred, always preceded wallowing.

Females entered pits in which bulls had urinated 39 times. They were observed wallowing 37 times (95%), and splashing 25 times (68%). The motor patterns used by females to splash urine onto the head and neck appeared to be identical to those used by bulls.

Female-Male Contact

We observed 40 instances in which females initiated physical contact with males during the rutting season (Table 1). Eleven were nose-to-nose contact, which is a greeting behavior common in many ungulates (Klingel 1977, Walther 1984), is performed year-round (pers. obs.) and may not have been associated with olfactory attraction. We have therefore deleted it from our analysis. Of the remaining 29 observations, 15 involved only nasal contact; in 14 instances females actually rubbed parts of their bodies against a bull. The distribution of contacts (both nasal and rubbing) differed from that expected if females randomly selected a part of the male to smell or rub against (chi-square goodness-of-fit = 15.2, $P < 0.01$). Of the 29 contacts, 62% were directed to the body of the adult bull. Females made contact with a bull's bell less than expected by chance.

Bell Morphology

Bell shapes were sexually dimorphic (chi-square = 119.2, $P < 0.001$). Adult females characteristically had bell types smaller than those of

TABLE 1. Actual and expected (based on chi-square analysis) distribution of cow physical contact (nasal and rubbing) with anatomical parts of bulls' bodies during the rut in Denali National Park, 1983.

TYPE OF CONTACT	AREA OF BULL BODY WITH WHICH COW MADE CONTACT					
	NOSE	POSTERIOR BODY	CHEST, NECK & BELL	ANTLERS	GENITAL REGION	TOTAL
NASAL	11	9	0	3	3	26
RUBBING	0	9	3	0	2	14
TOTAL	11	18	3	3	5	40
EXPECTED	--[a]	7.25	7.25	7.25	7.25	29

[a] Not included in analysis.

TABLE 2. Distribution of bell types by sex and antler size classes in Denali National Park, Alaska, 1982-1984.

SEX	ANTLER CLASS	BELL SHAPE[1] 1	2	3	4	5	6	7	8	TOTAL
MALE	1	0	0	0	7	5	0	0	0	12
	2	0	0	0	2	11	2	0	0	15
	3	0	0	0	0	6	10	0	2	18
	4	0	0	0	0	2	2	3	11	18
	5	0	0	0	0	3	0	10	14	27
MALE TOTAL		0	0	0	9	27	14	13	27	90
FEMALE		31	21	3	21	0	1	0	0	58

[1] See Fig. 1.

those of adult males (Table 2). The type of bell males carried was related to antler size (Table 2) (chi-square = 111.1, $P < 0.001$). Small antlered males tended to have bells that included a long tail (classes 4 and 5), while large-antlered males carried large, pendulous bells with little or no tail (classes 7 and 8).

Male-Male Interactions in the Antlered Period

Peek et al. (submitted) reported on 142 agonistic interactions between males at Denali National Park, using three antler classes. On no occasion were bulls of a smaller antler class dominant to bulls in a larger antler class. Because 84% of large-antlered bulls (antler classes 4 and 5) carried type 7 or 8 bells (Table 2), there is a strong association among large-antlered bulls, bell shape, and dominance during the antlered period.

Male-Male Interactions in the Antlerless Period

Agonistic interactions between bulls in the antlerless period and early stages of antler growth were observed 29 times (Table 3). An association between bell shape and dominance was first sought by sorting bell classes into two groups: those most often associated with small-antlered bulls (bell types 4, 5 and 6), and those associated with large-antlered bulls (bell types 7 and 8). No relationship between bell type and dominance was noted in this analysis (chi-square = 0.14, $P > 0.05$). Many interactions (43%) occurred between individuals with the same bell shape. A chi-square test based solely on interactions between the 2 bell subgroups (4, 5 and 6 versus 7 and 8) also failed to show a relationship between dominance and bell shape during the antlerless period

TABLE 3. The outcome of agonistic interactions between bull moose during the antlerless/early growth period (Jan. 1 to June 15) in relation to bell morphology, Denali National Park.

SUBMISSIVE ANIMAL	DOMINANT ANIMAL BELL TYPE				
BELL TYPE	5	6	7	8	TOTAL
5	1	1	4	1	7
6	0	11	2	1	14
7	5	1	0	4	10
8	0	0	1	3	4
TOTAL	6	13	7	9	35

(chi-square goodness-of-fit = 0.29, $P > 0.05$). One large-antlered male retained a type 5 bell throughout his life, and was dominant in 5 of 5 observed interactions during the early growth period. If he is deleted from the analysis, there is a significant tendency for animals with bell types 7 and 8 to be dominant over bell types 5 and 6 (chi-square goodness of fit = 6.2, $P < 0.05$).

Female-Female Interactions

We observed 107 agonistic interactions between cows in which dominance appeared to be established (Table 4); 90 interactions occurred during the rutting season. We found no correlation between dominance and bell type (chi-square = 8.6, $P > 0.05$) for three of the four bell types carried by cows (bell type 3 was omitted due to small sample size). We also tested whether the relative size of bells was related to dominance by comparing

TABLE 4. The outcome of agonistic interactions between female moose in relation to bell morphology, Denali National Park.

SUBMISSIVE ANIMAL	DOMINANT ANIMAL BELL TYPE				
BELL TYPE	1	2	3	4	TOTAL
1	1	4	0	5	10
2	5	13	1	29	48
3	1	1	0	7	9
4	9	18	1	12	40
TOTAL	16	36	2	53	107

outcomes of interactions between cows with noticeably different bell sizes. Of 103 interactions in which relative size was recorded, 75 occurred between cows with obvious differences in bell size. Relative bell size was not related to dominance in observed interactions (chi-square goodness-of-fit = 0.12, $P > 0.05$).

Female-Male Interactions

With the exception of yearling males, all bulls were dominant to cows during the antlered period (unpubl. data). During the antlerless period and early stages of antler growth, we observed 20 interactions (Table 5). Males with bell types 5, 7, and 8 were dominant on 12 occasions; males with type 5 bells were submissive to adult females in 8 interactions, including 4 that involved yearling males.

TABLE 5. Agonistic interactions between bull and cow moose during the antlerless/early growth period.

	MALE BELL TYPE					
	4	5	6	7	8	TOTAL
MALE DOMINANT	0	7	0	3	2	12
FEMALE DOMINANT	0	8	0	0	0	8

DISCUSSION

The Bell As An Olfactory Communicator

Our observations suggest that females are highly attracted to the urine of bulls. When bulls urinate in pits, females will frequently rush to the pit and aggressively compete for access. Females will occasionally make direct nasal contact as a male urinates.

The facts that both sexes have similar splashing behavior, and that the bell is closest to the urine puddle support the hypothesis that animals are attempting to impregnate their bells with urine. Because splashing by males is more commonly performed, and precedes wallowing in the behavioral sequence there is evidence that impregnation of the head region may be more important than the body. However, wallowing was more common for females. Contrary to what has been seen for wapiti (Struhsaker 1967) wallowing by moose rarely includes rubbing of the neck or bell directly in the pit; the body is the primary recipient of odor during this behavior.

Female-initiated contact with males during the rut has been reported for other cervids (Morrison 1960, Geist 1981, 1982), and interpreted as

arousal elicitation. Because cow moose appear highly attracted to bull urine, and because the entire body of a bull is impregnated with urine during the rut, we believe cow-initiated contact with bull moose is largely a result of female attraction to the odor.

If the bells of bulls were the primary carriers of chemical cues during the rut, and transferral of information occurred through direct contact, we would expect females, while making physical contact with males, to direct a large proportion of their attention to the bell. Instead, with the exception of nose-to-nose contact, cows primarily focused attention on the male body, usually the flanks and rear part of the male. Females may avoid direct contact with the anterior part of males because of the threatening presence of antlers. Males do chase females during the rut, and occasionally direct antler threats towards them (unpubl. data).

There is no evidence females impregnate themselves with male urine primarily through direct contact with the bull's bell. Impregnation appears to be achieved primarily through splashing and wallowing behavior, and secondarily through contact with males, including only occasional contact with the bell. Neither wallowing nor rubbing effectively impregnates the female bell. We therefore reject the hypothesis that the bell evolved as a transferral site for olfactory cues.

It is possible that the bell acts as an organ for scent dispersal rather than transfer. Elongation of hairs, or an increase in surface area of hair, is common on body parts where scent-urination is directed (Coblenz 1976), and apparently provides greater area from which volatile compounds can be released. The moose bell of both sexes probably does hold urine received from splashing. However, splashing is not highly site specific -- the neck, head and antlers (of bulls) all receive urine. Given the facts that, through splashing and wallowing, the whole body acts as a scent disperser, and that behavioral mechanisms used for impregnation are not site specific, it is questionable whether selection pressures on moose would be intense enough to encourage development of a specialized, site specific scent-dispersal organ.

The Bell As A Visual Communicator

Timmermann et al. (1985) reported that females possessed shorter, less conspicuous bells than males, that young males (2-4 years of age) had the longest bells, and that older bulls had broader, shorter bells with little or no tail. If we assume that bull age and antler size are correlated (Gasaway et al 1985), our results agree closely with those of Timmermann et al. (1985). The correlation between populations suggests that, as Timmermann (1979) has proposed, bell shape is a visual cue that transmits information about an animal's sex and age, and therefore possibly its relative rank. With our data on social interactions, it is possible to consider what kinds of information might be transmitted, and when such information transferral would be most advantageous.

We have no evidence that female bell shape or size is correlated with a dominance heirarchy among females. While such a heirarchy may exist, it does not appear that bell shape contributes to information transferral during female-female interactions. Dominant females in agonistic interactions are usually in a frontal orientation. Head high displays, kicking, and flailing, the most frequently observed behaviors, are performed directly towards an opponent, who would have little opportunity to see the bell and use the information to assess relative dominance. We

saw little evidence that females display or provide warnings before initiating aggressive acts--such behaviors appear suddenly and relatively unpredictably. Bell shape would seem to provide little information before or during such interactions. Therefore, if female bell shape transmits information, it is likely directed towards males.

Our observations of male-male interactions in the antlerless period are limited in number. Furthermore, they are confounded by the presence of one large-antlered, large-bodied individual who carried a type 5 bell through his entire life, and was dominant in all observed interactions. An increased sample size may demonstrate that certain bell shapes are associated with dominance during the antlerless period.

Timmermann (1979) suggested that bell shape may be most important in denoting rank during the antlerless period. The advantage of retaining a dominance heirarchy in winter appears questionable in light of the following evidence (unpubl. data) in Denali National Park: 1) social interactions are rare in winter; 2) bulls with class 7 and 8 bells (dominant animals most likely to gain from such a heirarchy) are largely solitary in winter, and when associating with other animals, usually do so with other bulls that carry type 7 and 8 bells; 3) antlerless males use the same behaviors as do females in agonistic interactions, which, as noted above, do not easily allow assessment of relative dominance by bell morphology, and; 4) if a dominance heirarchy is maintained, there should be some advantage to its maintainence, i.e., rank confers access to some limited resource (Wilson 1975). In winter, the only advantage may be access to feeding sites, as has been demonstrated for red deer (Appleby 1980). In highly social cervids, such as red deer and elk, antlers are retained through the winter, and dominant animals do accrue benefits by appropriating feeding sites. Of the interactions we have observed, few appeared to be associated with access to feeding sites.

We believe that, if bell morphology is used as a visual cue, it is most important during the rut, the time when interactions are most frequent, intensity of interactions is greatest, sociality is greatest, and clear signals of social status directly affect reproductive success. In contrast to interactions between antlerless moose (males and females), male-male interactions during the antlered period include displays that allow broadside views of the head and neck. Behaviors such as the antler threat, parallel walk (challenger gait), and broadside display include partial or complete lateral presentation that provide a profile of antlers and bell shape. All displays develop relatively slowly, and give recipients the opportunity to assess relative status. A submissive animal will often turn its head away from an opponent, also providing a broadside view of the bell and antlers.

There is a marked degree of sexual dimorphism in bell morphology. Female bell size varies considerably, but is consistently smaller than that of adult males. Overlap in bell morphology occurs only between adult females and yearlings or small-antlered bulls. We hypothesize that small bell size (types 1-4) represents low ranking or juvenile social status. Medium-sized bulls carry a bell with a large body (type 5), as do large-antlered bulls. However, the long tail associated with the bell is prominent, and acts as a visually obvious cue that separates the 2 classes. Type 6 bells represent an intermediate phase between large-antlered, breeding class bulls, and medium-sized bulls. The tail has been lost, but the dewlap portion of the bell has not noticeably enlarged. Bell types 7 and 8 appear to be slightly different

representations of the same social status.

Secondary sexual characteristics that reduce the potential for misidentification during rutting interactions would be advantageous to all individuals. Because escalated combat between males is energetically costly and the potential for injury is high (Geist 1971, Clutton-Brock et al. 1979), any visual feature that minimizes the potential for physical conflict would be reinforced through natural selection processes. Dominant bulls who clearly advertise their status minimize energy expended to retain dominance. By visually acknowledging subordinance, submissive males benefit by reducing the chance of incurring injury from a dominant, and can remain with or in close proximity to other animals, thereby reducing the risk of predation (Hamilton 1971) and increasing the potential for breeding if the opportunity arises. In male-female interactions it is to the advantage of females to advertise their status because females wallow in male urine, often of a dominant bull, and therefore present a mixed representation of sex and social status. Presence of an obvious visual cue -- no antler and a small bell -- may avoid misidentification based on olfactory cues. As suggested by Timmermann (1979), physical characteristics other than antlers that advertise social status may be important because: 1) moose are active during the night when visibility may not be good, and; 2) moose are often in dense vegetation (forests or shrublands) that may partially obscure antlers, and make accurate assessment, based on antlers only, difficult.

It has been hypothesized that morphological changes in bell shape are a result of freezing and loss of the tail of a bell during the winter (Franzmann 1981, Timmermann et al. 1985). We propose that an understanding of the mechanism involved in the loss of the tail can be used to test the hypothesis that bell shape is an important component of moose visual communication. If bell shape or loss of a portion of the bell had an effect on survival or reproductive success, natural selection would act to retain critical features of bell shape, regardless of weather conditions. We propose that the evolution of a social organ used for visual communication that was susceptible to frostbite would be unlikely in an animal that evolved in and presently inhabits areas with harsh environmental conditions. If there exists selection for changes in bell morphology, frostbite may be the proximate cause of a mechanism that has a physiological basis. The hypothesis that frostbite alone regulates bell shape of males can be tested by comparing moose populations in areas with extremely cold winters (Denali and Ontario) to areas where winter temperatures would not be sufficiently extreme to cause frostbite.

CONCLUSIONS

Homologous beard-like organs of ungulate species other than moose are apparently used both as visual and olfactory communicators (Coblentz 1976, Lott 1979). Our data allow us to reject the hypothesis that the male bell provides a mechanism for transfer of chemical stimuli through direct contact, and suggest that the bell is no more important than other parts of the body for scent dispersal. Available evidence suggests that bell shape is not related to rank among females, nor among males during the antlerless period. The presence of antlers, and their possible role as visual stimuli, makes determination of the importance of bell shape during the rut difficult. Future work will be devoted to determining the association between rank and bell morphology in the fall, and comparing bell morphology of populations in varying environmental regimes.

ACKNOWLEDGEMENTS

We thank John Dalle-Molle and the staff of Denali National Park and Preserve for cooperation and logistical support. J. Byers and two anonymous reviewers provided helpful comments.

LITERATURE CITED

APPLEBY, R.C. 1980. Social rank and food access in red deer stags. Behaviour 74: 294-309.

BARTOS, L., and J. HYANEK. 1983. Social position in the red deer stag II. The relationship with developed antlers. Pages 463-466 in R.D. Brown, ed. Antler development in Cervidae. Caesar Kleberg Wildlife Research Institute, Kingsville, TX.

BUBENIK, A.B. 1983. The behavioral aspects of antlerogenesis. Pages 389-450 in R.D. Brown, ed. Antler development in Cervidae. Caesar Kleberg Wildlife Research Institute, Kingsville, TX.

_______. 1983. Behavioral significance of the moose bell. Alces 19: 238-245.

CLUTTON-BROCK, T.H., S.D. ALBON, R.M. GIBSON, and F.E. GUINNESS. 1979. The logical stag: adaptive aspects of fighting in red deer (Cervus elaphus L.). Anim. Behav. 27: 200-225.

CLUTTON-BROCK, T.H., F.E. GUINNESS, and S.D. ALBON. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago. 378 pp.

COBLENTZ, B.E. 1976. Functions of scent-urination in ungulates with special reference to feral goats (Capra hircus L.) Am. Nat. 110: 549-557.

FRANZMANN, A.W. 0980. Frostbite. Pages 220-223 in Dieterich, R.A., ed. Alaska wildlife diseases. University of Alaska, Fairbanks.

GASAWAY, W.C., D.J. PRESTON, D.J. REED, and D.D. ROBY. 0985. Comparative antler morphology and size of North American moose. Viltrevy. In press.

GEIST, V. 0963. On the behaviour of North American moose (Alces alces andersoni Peterson 0950) in British Columbia. Behaviour 20:377-406.

GEIST, V. 0966. The evolution of horn-like organs. Behaviour 27: 075-204.

GEIST, V. 0970. Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago. 383 pp.

GEIST, V. 0980. Behavior: adaptive strategies in mule deer. Pages 057-224 in Wallmo, O.C., ed. Mule deer and black-tailed deer of North America. University of Nebraska Press, Lincoln..

GEIST, V. 0982. Adaptive behavioral strategies. pp 209-278 in Thomas, J.W., and D.E. Toweill, eds. Elk of North America: ecology and management. Stackpole Books, Harrisburg, PA.

HAMILTON, W.D. 0970. Geometry of the selfish herd. J. Theor. Biol. 30:295-300.

KLINGEL, H. 0977. Communication in perissodactyla. Pages 705-727 in Sebeok, T.A., ed. How animals communicate. Indiana University Press, Bloomington.

LOTT, D.F. 0974. Sexual and aggressive behavior of adult male American bison (Bison bison). Pages 382-394 in Geist, V., and F.R. Walther, eds. The behavior of ungulates and its relation to management. IUCN New Series Publ. 24, Morges, Switzerland.

_______. 0979. Hair display loss in mature male American bison: a temperate zone adaptation? Z. Tierpsychol. 49: 71-76.

LYDEKKER, R. 0903. Catalogue of the ungulate mammals, Vol. 0, Artiodactyla. British Museum, London.

MORRISON, J.A. 0960. Characteristics of estrus in captive elk. Behaviour 06:84-92.

PEEK, J.M., V. VAN BALLENBERGHE, and D.G. MIQUELLE. Submitted. Intensity of interactions between rutting bull moose in central Alaska. J. Mammal.

PETERSON, R.L. 0955. North American moose. University of Toronto Press, Toronto. 280 pp.

SCHALLER, G.B. 0967. The deer and the tiger: a study of wildlife in India. University of Chicago Press, Chicago. 370 pp.

SHANK, C.C. 0972. Some aspects of social behavior in a population of feral goats (Capra hircus L.). Z. Tierpsychol. 30:488-528.

STRUHSAKER, T.T. 0967. Behavior of elk (Cervus canadensis) during the rut. Z. Tierpsychol. 24: 80-004.

TIMMERMANN, H.R. 0979. Morphology and anatomy of the moose (Alces alces L.) bell and its possible functions. M.S. Thesis, Lakehead University, Thunder Bay, Ontario. 82 pp.

_______, M.W. LANKESTER, and A.B. BUBENIK. 0985. Morphology of the moose bell. Alces 20. In press.

WALTHER, F.R. 0977. Artiodactyla. Pages 655-704 in Sebeok, T.A., ed. How animals communicate. Indiana University Press, Bloomington.

_______. 0984. Communication and expression in hoofed mammals. Indiana University Press, Bloomington. 423 pp.

WILSON, E.O. (1975. Sociobiology: the new synthesis. Harvard University Press, Cambridge, Mass. 697 pp.