BEHAVIOURAL SIGNIFICANCE OF THE MOOSE BELL

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Abstract: It is hypothesised, through observation, that the primary function of the bell of moose (*Alces alces*) is to disseminate and transfer by contact, the urinary and possibly salivary pheromones of the bull close to or directly on the nose area of the cow. The large surface area and higher amount of sebum of the bell, in comparison with that of the cow, enables retention in the hair of great amounts of pheromones and deceleration of evaporation of those which are bipolar. The cow searches for these pheromones on the tongue, lips and nose area of the bull by: (1) direct contact when the bull urinates; (2) more frequently by rubbing her face all over the bell and adjacent parts of the throat which are impregnated by urinary pheromones from the rut-pit-hole; (3) by rubbing her chin and cheeks in the fresh pithole. By this way her smaller, tail-shaped bell is impregnated and becomes a reservoir of pheromones, swinging close to the nostrils, when the cow is running. Since both sexes produce the same urinary pheromones during estrus, a very effective mutual stimulation of gonadal activity and synchronization of estrus of the cows around the bull is thus achieved. This is considered as a necessary prerequisite for short, successive and economic mating strategy in the tundra, probably the original habitat of the moose.

Despite the careful anatomical, morphological and histological investigation by Timmermann (1979) the sociobiological significance of the bell remains obscure. The fact that its organogenesis begins in both sexes in very early stages of fetal development (Knorre 1959, Timmermann 1979) and that the shape of the bell becomes sexually dimorphic when sexual maturation is achieved (Timmermann 1979) gives evidence towards its sociobiological importance.

The very pronounced vascularization (Timmermann 1979) seems to be a necessary adaptation for avoiding hypothermy of this very exposed "skinny" appendage. The tail-shaped bottom of the bell-mostly in bulls-generally freezes off in the second winter (Knorre 1959, Timmermann 1979). Why this happens more frequently in the woodlands than in open tundra (Timmermann 1979, Bubenik unpubl.) is unknown. Then, by no means can the tail-shaped bell of bulls be considered a characteristic for *Alces a. gigas* and the sack-like for the other North American subspecies, as suggested by Geist (1982).

Sokolov (1964) and Timmermann (1979) point out that the bell skin has relatively dense sebaceous and eccrine sweat glands, while the presence of apocrine glands remains questionable.

Hair patches, hair stripes or long hairs on the neck are developed in some cervids and many bovids (Haltenorth 1963) that are sometimes associated with enlarged and very long tubule of sebaceous glands (Schaffer 1940). In some species of *Capra* or in *Onotragus* (Walther 1977) and in *Cervus sp.* (Bubenik unpubl.) the males impregnate these hairs with urinary pheromones discharged directly on the down-bowed throat, by rubbing them on vegetation, or in wallows moistened by their urine.

In moose it is known that the bull paws the pitholes in which both sexes wallow (Thompson 1949, Lent 1975). However, I suspect that the cow of woodland moose can also paw pitholes which are very shallow.

Zschetzsche (1959), in a rather confusing report, stated that the unpleasant odour of the bell originates from constituents of secretory glands with an orifice at the bottom of the bell. However, no such orifice can be found in moose (Timmermann 1979).

The penetrating odour of moose in estrus is composed of cresols, phenols, esters and other aliphatic and aromatic, mostly bipolar, compounds, as originally isolated from swabs of the tarsal gland, and originally described as their secretion (Bubenik et al. 1979, Dombalagian 1979). Dombalagian (pers. comm. 1982) has shown that these substances are present in the urine of both sexes in estrus. With these findings, it is not know if the tarsal glands produce the same substances and we must accept the main source of the odour as urine.

The bipolarity of most of the urinary pheromones has the advantage that they can interact with the wet surface of the hair of the bell and with the sebum. In this way they spread over the bell and their volatility is substantially reduced (Regnier and Goodwin (1977). Thus, the bell becomes a lasting disseminator and reservoir of urinary pheromones.

MATERIAL AND RESULTS

The fact that the estrual pheromones are the same for both sexes may mean that they operate simultaneously as primer, releaser and informer (Muller-Schwarze 1977) and have a powerful stimulating effect when present in the air. The bell of the moose seems to have evolved for this purpose, as has been well demonstrated in J. L. Frund's movie "The High Season of Moose", from which some of these observations originate.

The scent of the bull's urine is very attractive for any cow approaching the estrus phase. The urinating posture of the bull, or the sound of urination, is a cue which forces the cow to approach the bull and the pithole. From the behaviour of cows around the bull I conclude that the urinary pheromones have a priming effect on the cow, inducing her estrus and attractive phase (Beach 1976). As soon as the cow enters the proceptive phase, she tries to come in direct contact with bull's urine, pushing her nose in the urine stream and/or sitting in the pithole, rubbing her chin, bell and cheeks to impregnate them with the urinary pheromones. The bull does the same, however in two distinct steps. First, he stamps in the pithole so vigorously that the urine and dirt are splashed on the neck, bell and dorsal side of his antlers, followed by bedding down in the pithole and rubbing the bell.

The cows usually circle the pawing and pithole-bedded bull, and those in the proceptive or receptive phase try to come into intimate contact with the bull. When the bull stands, a cow in the most advanced estrus will begin to rub her face and head on the bell and throat of the bull and let the bull lick her vagina and put his bell and chin on her pelvic region. Finally a mutal rubbing of heads, not unlike caressing, is performed.

The cow in receptive phase dominates all others. However, if more than one is in this status, a direct competition with threats and front leg beating will start in order to assert the hierarchy and the right to be courted.

If my observations are correct, I have to assume that the cow tries to lick the musky smelling saliva from the bull's chin. If this is true, then it might be that the heavily salivating bull is discharging

5 alpha-androst-16-en-3-one with his saliva, a steroidale substance. This can be reduced into the two musky androstenediols, both very powerful sex pheromones, as has been found in the boar (*Sus spp*) (Claus et al. 1971) and to a lesser amount in red deer (*Cervus elaphus*) (Claus, pers. comm. 1980).

The bell of the cow is her own reservoir or urinary and possibly salivary pheromones. By stronger head movements the tail-shaped bell undulates and disseminates the odour around her nostrils, keeping the stimulation constant, even if the cow is out of range of perceiving a bull.

The question of the advantage of the tail-shaped bells in mature bulls arises. Its surface, and of course the amount of sebum as a solvent for pheromones, is larger than in the sack-like bell. Therefore the tail-shaped bell should be a better odour disseminator than the sack-like bell. This would be advantageous in open country which I consider the primary habitat (Bubenik 1973), where the scent is carried much farther than in woodland. The fact that in open country the tail-shaped bell of bull moose is more frequently seen than in the taiga (Timmermann 1979) might be considered either as incidental or purposive.

The polygynous breeding strategy of tundra moose affords very effective mutual stimulation and synchroization of estrus. Such stimulation is less important in the taiga due to serial monogamy and spatial separation of cows (Bubenik 1983, in press).

CONCLUSION

Moose, as an absolute individualistic species (Bubenik 1983, in press, Houston 1974) have a breeding strategy in which the bull is monopolized

by the cow, and therefore it does not matter if the mating is polygynous or serially monogamous. Sex pheromonal stimulation for both sexes is advantageous in either case. For cow assemblages the primary function may be the synchronization of estrus. In monogamous mating it may serve to aim the gonadal stimulation of the bull, whose relatively low testicular activity (Bubenik and Timmermann 1983) may need effective stimulation due to the excessive copulatory activity of this strategy (Bubenik 1983, in press).

Finally, the bell as a disseminator and reservoir of the urinary pheromones is advantageous to such tall animals, whose nose is generally kept high above the ground and ground vegetation.

The hypothetical conclusion supports the view of Timmermann (1979) that one of the functions of the bell of the moose may be the olfactory.

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