VASCULARIZATION OF THE MOOSE BELL

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ABSTRACT: The vascularization of the moose (*Alces alces*) bell was examined by gross dissection following injection of vinyl acetate into the arterial and venous systems and by radiological photography. In a total of 28 heads, the bell artery originated from the left lingual artery in 15 (10 males, 5 females) and from the right in 13 (8 males, 5 females). The bell artery runs distally giving off a major branch to the dewlap and continues into the tail portion of the bell. The bell vein (3-5 mm lumen diam.) originates in a capillary bed in the distal portion of the bell and runs proximally, adjacent to the bell artery. It receives one or two major branches from the dewlap and joins either the right or left jugular vein in the lower neck. We suggest that a change in bell shape results from a portion being lost by freezing due to limited vascularization in the bell tail.

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The bell on moose is a hair-covered fold of skin extending ventrally from the intermandibular area and hanging free from the throat region in both sexes (Gunderson and Beer 1953; Burt 1957; Cahalane 1961). It is found on all seven races of moose world wide (*A. a. americana, A. a. andersoni, A. a. shirasi, A. a. gigas, A. a. alces, A. a. pfizenmayeri and A. a. cameloides*) (see Seton 1929; Peterson 1955; Van Wormer 1972; Franzmann 1978; and, Lee Rue and Owen 1985).

Much speculation has been focused on the possible function of the bell. Both Fitzinger (1874) and Zschetzche (1959) suggested an olfactory communications role, however several other explanations have been offered to interpret its presence. Vereshchagin (1967) believed it helped to protect the gullet from excessive cold when moose bedded on the snow. Herrick (1892) implied its purpose was purely ornamental. Seton (1929) and Bubenik (1973) speculated that the bell in present day moose may be a vestigial organ which, through evolution, has lost its function and no longer serves any useful purpose. Bubenik (pers. comm. 1977) later suggested the bell may be a thermoregulatory organ or a useful secondary indicator of sex and age as proposed by Timmermann *et al.* 1985.

The bell is sexually dimorphic being longer and having a greater profile area on male than on female moose (Timmermann 1979, Miquelle and Van Ballenberghe 1985, Timmermann *et al.* 1985). On bulls, the longest bells occur on animals 2-4 years old. With increasing age, the proximal, dewlap portion of the male bell broadens and the pendulous tail portion decreases in length. The tail of the bell on some older males is lost as evidenced by a tissue scar at the bottom of all sac-shaped bells. It has been suggested that the tail is lost as a result of freezing (Timmermann 1979, Franzmann 1981, Timmermann *et al.* 1985).

In behavioral studies by Miquelle and Van Ballenberghe (1985), no correlation was seen between relative size of the bell and social dominance among females at all times of the year or among males during the anterless period (January-June). Their confidence in this conclusion regarding males was limited because of small samples and one dominant individual with an intermediate-classed bell. There was a strong association among large antler size, bell shape and male dominance during the antlered period. Dominant males had the largest antlers and a tail-less, sac-shaped bell.

Miquelle and Van Ballenberghe (1985) favoured the hypothesis that bell shape is a secondary sexual characteristic, likely of greatest importance during the rut in conveying visual information about social status. They also thought it unlikely that a shape-specific social organ of this type, selected by a northern adapted animal, would be susceptible to frostbite. Instead, a frostbite-induced change in shape may have a physiological basis (Miquelle and Van Ballenberghe 1985).

The purpose of this study was to describe the vascularization of the moose bell in an attempt to better evaluate some of the above suggestions made by previous authors.

METHODS

The vascularization of the bell was examined by gross dissection following the injection of vinyl acetate (Ward's Natural Science Establishment, Inc. Rochester, N.Y.) into the arterial and venous systems and by X-ray photography. Whole heads, freshly killed or frozen, were left at room temperature (20°C) for several days allowing clotted blood in vessels to liquify. A teflon medicut (Argyle Co.) with a 12 guage cannula was inserted into one of the carotid arteries and tied in place. Fluid was injected using a 50 cc syringe. Initially, a small volume (100 cc) of saline was injected to force remaining blood out the opposite carotid or from the tip of the bell which had been cut off. Formalin was then injected and left for 15 minutes before injecting acetone followed by red vinyl acetate. If resistance to the acetate injection was encountered on one side of the head, the carotid artery on the opposite side was injected. Finally, the carotids were tied off and hemostats clamped on the bell tip to prevent leakage from the vessels. A similar procedure was used in injecting barium sulphate (suspension of Barosperse, Mallinckrodt Corp.) prior to making radiographs. The venous system on several specimens was traced by exposing both anterior sublingual veins and back injecting with blue vinyl acetate. In addition, some were injected near the tip of the bell tail.

Double injected heads with skin removed were placed in a 10% solution of potassium hydroxide to remove soft tissue and expose a cast of the circulatory system. In addition, a number of selected bells severed from heads were injected with vinyl acetate and barium sulphate using #21 butterfly needles attached to a 10 cc syringe. The soft tissue of vinyl acetate injected bells was digested in a 5% solution of sodium hydroxide at 60°C for 48 hours.

Those injected with barium sulphate were radiographed along with barium injected heads at McKellar General Hospital in Thunder Bay using a Picker 300 MA potable X-ray machine. Dupont chronex 4 film, size 36 x 92 cm, with Hi plus screens and a grid were used. Whole heads required an exposure time of 14 seconds at 70 KVP, 15MA at a 2 metre focal length while X-rays of bell tissue were taken at 60 KVP, 15 MA for 1/2 second.

Tissue samples from the tail portion of the bell were examined histologically. Samples were cut transversely from the proximal, mid and distal regions of the bells of males and females of all ages. The tissue was fixed in buffered formalin, dehydrated in an ethanol series, embedded in parafin and cut at a thickness of 5-14 µm. The entire bell of mid-term and full-term fetuses was cut longitudinally. Scars visible grossly at the tip of bells were also examined histologically. Lillies a-b stain (Lillie 1954) and Harris' hematoxylin-eosin were used routinely.

RESULTS

Dissection of vinyl acetate injected bells revealed a single small artery (1.5-2.5 mm lumen diam.) designated the bell artery, arising ventrally from either the left or right lingual artery between the origins of the linguofacial and sublingual branches (Figs. 1

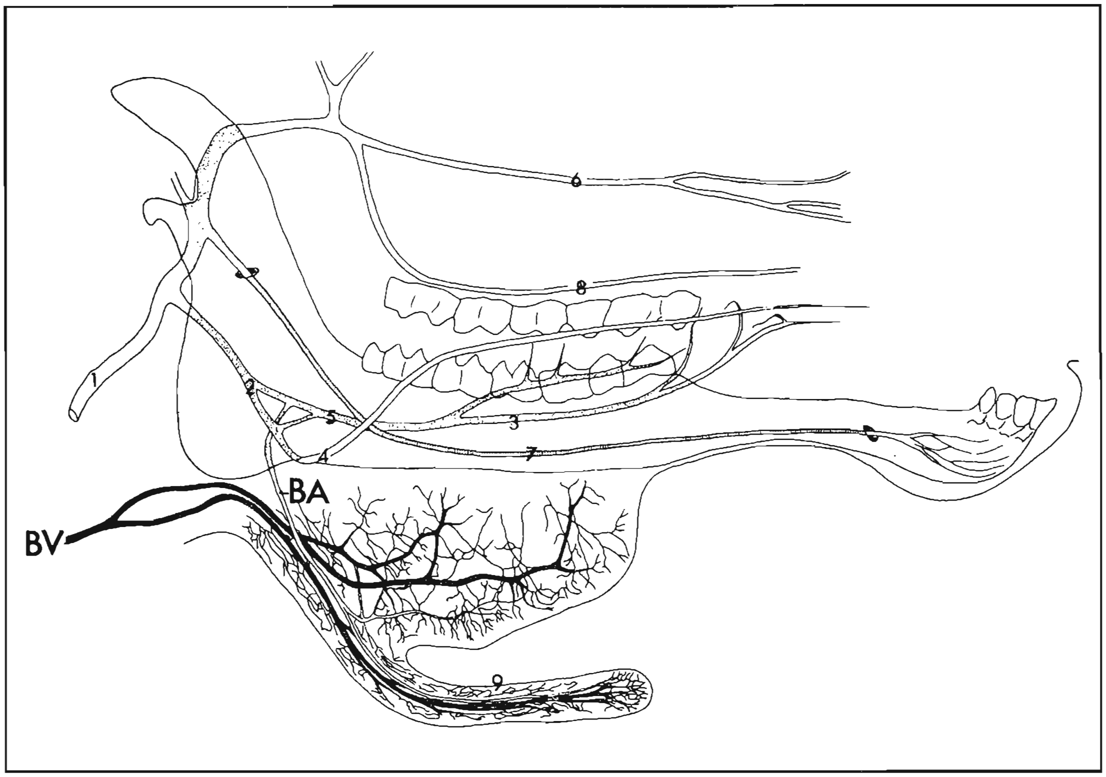


Figure 1. Vascular system of the head and bell of a moose, lateral view. **1** - common carotid artery; **2** - lingual-facial branch; **3** - sublingual artery; **4** - facial artery; **5** - lingual artery; **6** - infraorbital artery; **7** - mandibular-alveolar artery; **8** - maxillary artery; **9** - bell tail; **BA** - bell artery; **BV** - bell vein (Standard vascular system terminology after Sisson and Grossman 1953).

and 2). A total of 28 heads (18 males, 10 females) were injected specifically to confirm the apparent unilateral origin of the bell artery. The bell artery originated from the left lingual artery in 15 (10 males, 5 females) and from the right in 13 (8 males, 5 females). The bell artery gives off a major branch to the dewlap and continues into the tail portion of the bell.

Barium sulphate injected into the bell artery apparently was able to flow through the capillary bed and fill the venous system (Figs. 3 and 4). The bell vein (3-5 mm lumen diam.) originates in a capillary bed in the distal portion of the bell and runs proximally, adjacent to the bell artery and receives one or two major branches from the dewlap. At a point just below the angle of the mandible, the bell vein turns to run posteriorly just beneath the skin to join either the right or left jugular vein in the lower neck region. A male calf submitted whole, provided the single opportunity to follow the bell vein to its junction with the jugular vein. In this animal, the bell artery arose from the right lingual and the bell vein joined the left jugular.

In sac-type bells without a tail, the major arterial and venous circulation was similar to that found in the dewlap of bells with a tail (Fig. 4). There was usually a prominent network of small vessels in the region adjacent to the scar on sac-type bells but the branches of the bell artery and vein that serve the tail of typically shaped bells were not apparent.

The histological study is based on the examination of approximately 500 sections from 28 males and 12 females representing all age groups. The outer epidermal surface on

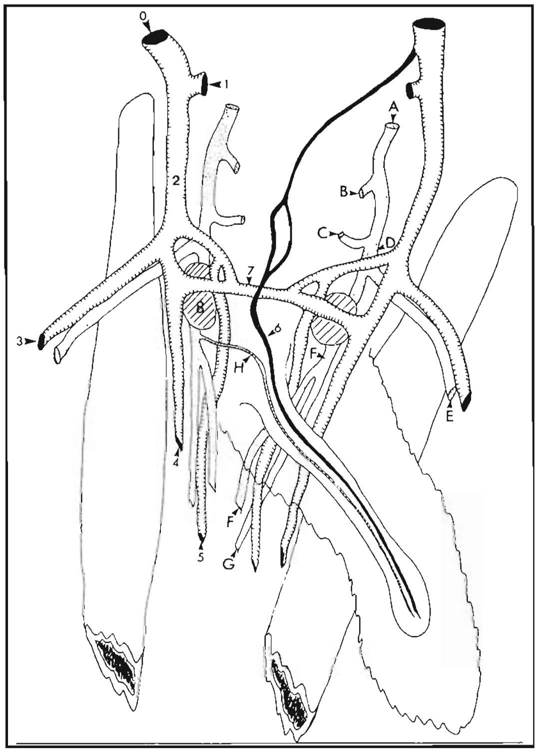


Figure 2. Deep dissection of the inter-mandibular area of a moose head (ventral view) showing major vessels. Venous: **0** - jugular vein; **1** - external maxillary vein; **2** - linguofacial vein; **3** - facial vein; **4** - sublingual vein; **5** lingual vein; **6** - bell vein; **7** - transverse vein; **8** - mandibular lymph node. Arterial: **A** - common carotid artery; **B** - internal carotid artery; **C** - maxillary artery; **D** - linguofacial artery; **E** - facial artery; **F** - lingual artery; **G** - sublingual artery; **H** - bell artery. (Standard vascular system terminology after Sisson and Grossman 1953).

bells of growing moose >0.5 yr typically is a thin (15-40 cm) layer of squamous epithelium, 2-5 nucleated cells thick, overlain by a superficial layer of keratin. Beneath the epidermis, the dermis composed of two layers presents a thin superficial papillary layer with fine-fibred irregular connective tissue and a deeper, thicker reticular layer of heavy, dense-fibred irregular connective tissue containing hair follicles, small blood vessels, sebaceous glands, errector pili muscles and a few elastic fibres and nerve endings. Beneath the deepest hair bulbs, the dermal layer forms a common central core of interwoven collagen fibres interlaced with larger blood vessels. The main bell artery and vein lead to a deep anastomosing network from which smaller blood vessels ascend to the upper dermis. Sweat glands, deeper sebaceous glands and hair bulbs are supplied by smaller side branches (arterioles, venules and capillaries). Vessels in the papillary layer supply smaller vessels which ascend into each of the dermal papillae.

Hair follicles penetrate diagonally into the dermis to a depth of 2.5 to 4.5 mm. A pattern of increasing dermal hair depth and density was observed from mid to distal portion of the tail. Two extreme sizes of hairs include long, large diameter (250 um) coarse guard hairs and shorter, finer, diameter (20-25 µm) hairs.

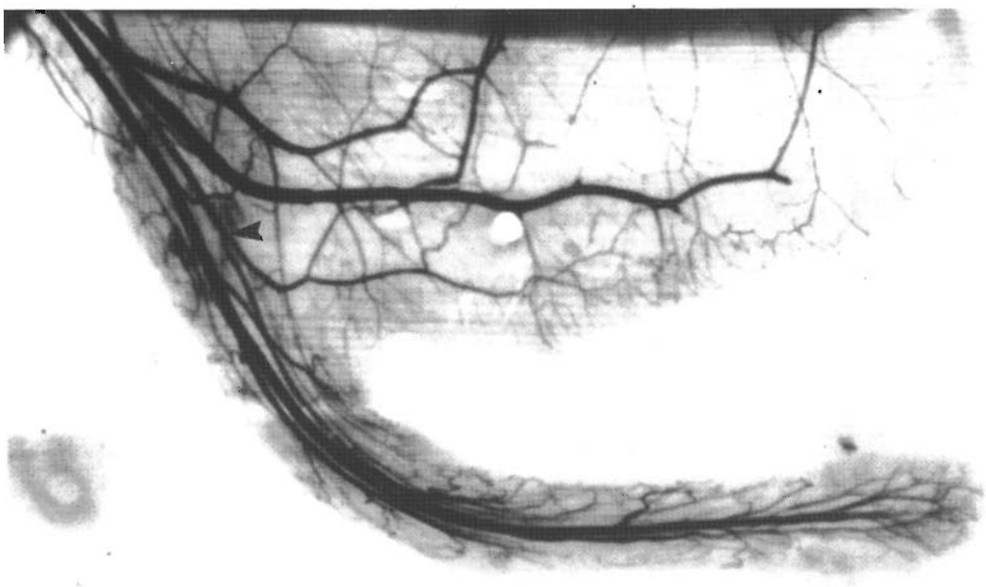
Histologically scars found on the distal tip of some bells consisted of glossy, elongated collagen fibres orientated at right angles to fibres in the adjacent undamaged dermis. The keratinized layer over the scar was thickened and hair follicles were absent.

The extent of arterial branching in the tails of two bells is illustrated by vinyl acetate casts (Fig. 5 and 6). Both histological examination and latex injections gave the impression that the narrow isthmus of the bell was less vascularized than either the proximal or distal regions.

DISCUSSION

Moose extremities (ears and bells) are often subjected to prolonged freezing ambient temperatures. Freezing generally causes destruction of superficial tissues and functional disturbance of small surface blood vessels (Siegmund 1973). Published reports of frostbite in wild mammals including moose, however, appear rare.

There is some evidence that the tail portion of the bell of moose may be lost as a result of freezing (Timmermann 1979, Franzmann 1981). This may be related to its length. Timmermann *et al* (1985) reported the tail portion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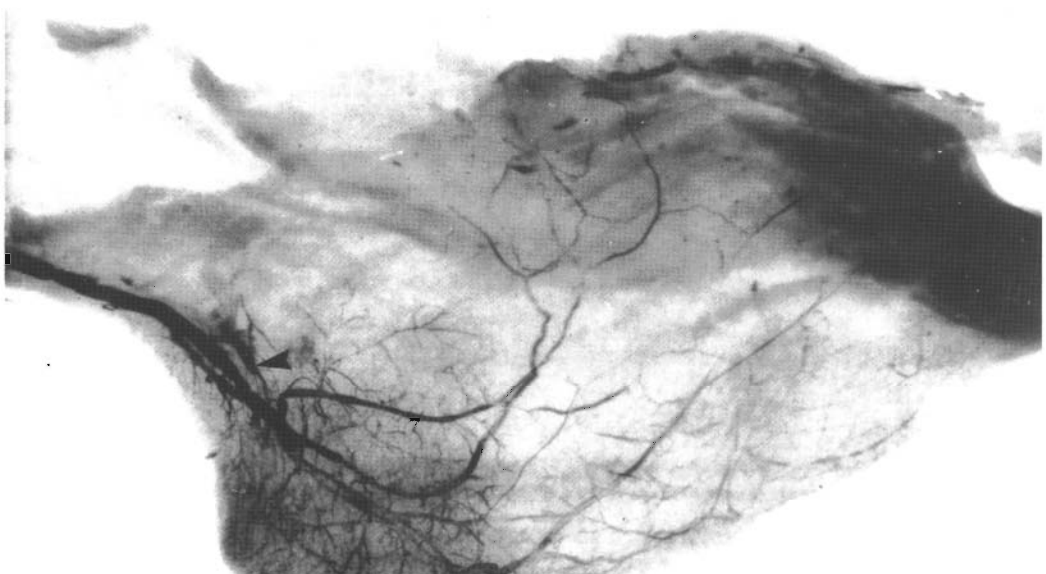
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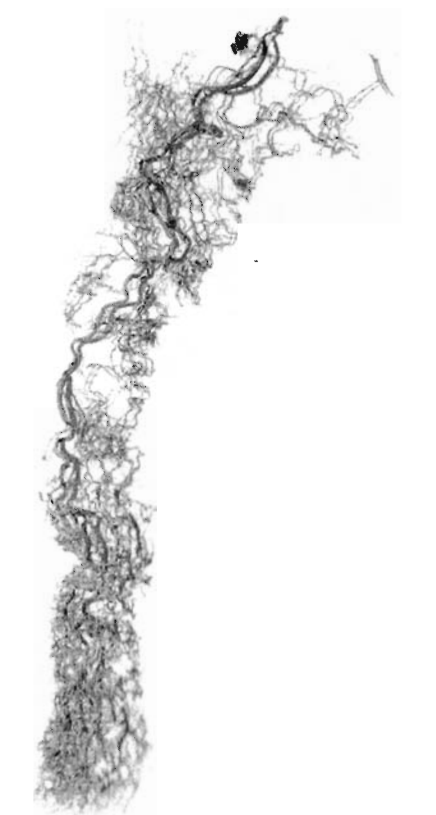
Figure 3. Radiograph of the vascular system of a tail-type bell from a 3.5 yr-old male moose. Approximately 1/2 original scale (◄ indicates bell artery).

Figure 4. Radiograph of the vascular system of a sac-type bell from a 15.5 yr-old male moose. Approximately 1/2 original scale (◄ indicates bell artery; > indicates scar on ventral edge of bell).



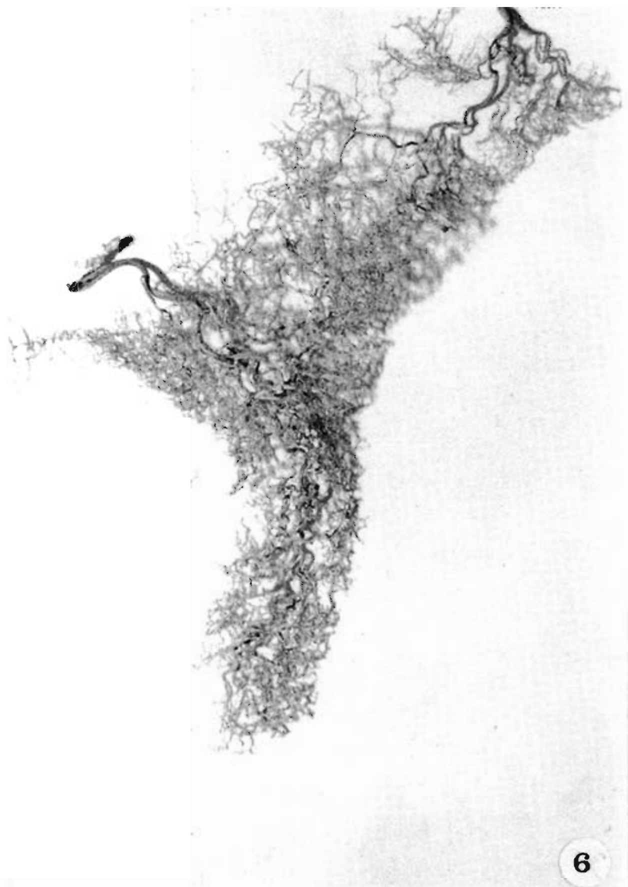


Figure 5. A vinyl acetate cast of the arterial system in the bell tail and a portion of the dewlap from a 3.5 yr-old, male moose. Approximately 1/2 original scale. Original bell length without hair = 38.8 cm, tail = 19 cm, bell profile area = 457 cm^2, dewlap = 401 cm^2, tail = 60.0 cm^2.

Figure 6. A vinyl acetate cast of the arterial system in the bell tail from a 2.5 yr -old, male moose. Approximately 1/2 original scale. Original bell length without hair = 51.0 cm, tail = 30.0 cm, bell profile area = 601 cm^2, dewlap = 535 cm^2, tail = 72 cm^2.

of the bell of Ontario moose (*Alces alces*) was generally longer on males than on females and loss of all or part of the tail was much more prevalent in males than in females. Franzmann (1981) reported most Alaskan moose (*Alces alces gigas*), particularly males, develop an extremely long bell in their early life. The elongated section of the bell tail is generally lost during the winter of the second to fourth year, but the base remains. The shortened bells of older Alaskan moose are believed to result from frostbite. Males >5 yr. examined by Timmermann *et al.* (1985) showed a higher incidence (52%, N=33) of a terminal scar than females (2%, N=43). Bells with a terminal scar had a significantly shorter tail ($P<0.05$) than those without a scar. Insulating winter hair was also least dense in the mid-region of the tail and sparsely-haired patches were commonly seen on the tail of exceptionally long bells. The mid portion of some long bell tails appeared less vascularized than either the proximal or distal regions.

We suggest frostbite is the causal agent in changing bell shape among male moose. Some animals may be unable to maintain suitable skin temperatures due to the limited vasularization, particularly in the proximal region of the bell tail. This hypothesis can be further tested by a more detailed histological comparison of male and female bells.

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