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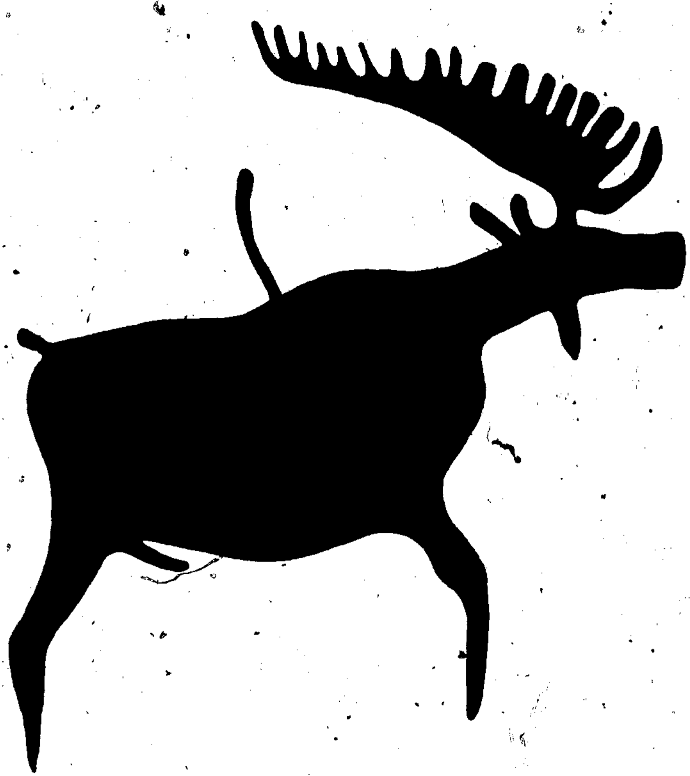
MORPHOLOGY AND ANATOMY OF THE MOOSE (*ALCES ALCES* L.) BELL AND ITS POSSIBLE FUNCTIONS

by

H. R. (Tim) Timmermann

A thesis
presented in partial fulfillment of the requirements for
the degree of Master of Science

Department of Biology, Lakehead University
Thunder Bay, Ontario
May, 1979



ABSTRACT

The bell is a conspicuous and unique structure hanging beneath the lower jaw of both male and female moose, *Alces alces* L. Sexual dimorphism was seen in the shape and size of the bell. Males demonstrated the greatest development and variation. The longest bells were found generally on young bulls 2 - 4 years old. The dewlap portion of the male bell broadened and the tail portion shortened with increased age. These morphological changes resulted partially from the loss of all or a portion of the bell tail, probably by freezing. Females generally possessed a shorter, less conspicuous bell than males. Bells on females older than 3.5 years changed little in their appearance with increasing age and were similar morphologically to bells on yearling males.

The density and rate of growth of hair on the bell were examined in relation to changing bell morphology and loss of the bell tail. The density of moose winter tick, *Dermacentor albipictus*, was higher on the distal tip of the bell (up to 11/cm^2) than recorded in the literature. The feeding activity of ticks may contribute to the loss of the bell tail through freezing.

The bell did not appear to be a specialized organ for glandular secretion. The bell consisted of an evagination of hair-covered skin united by a dermal core. Both sebaceous and eccrine-like sweat glands were present in skin of the bell but they did not differ in number or appearance from those elsewhere in general body skin.

The major blood vessels of the bell included a single bell artery which originated from either the left or right lingual and a bell vein joining either the left or right jugular beneath the skin in the upper neck.

The possible importance of the bell as a visual cue in social interactions is discussed but a definitive explanation of the function of the moose bell remains obscure.

ACKNOWLEDGEMENTS

I am grateful to the Ontario Ministry of Natural Resources for the opportunity to collect the data contained in this study and permitting me to take leave of absence to finalize my study at Lakehead University.

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Dr. A. B. Bubenik, originally suggested this research problem and after the program was initiated provided much advice, encouragement and personally translated European literature. Many people kindly helped me with the anatomical aspect and provided me with unpublished data. My thanks go especially to Dr. Hugh McIntyre, Mr. Brian Hewlett, Dr. Jean-Marc Klein, Mrs. Lynn Ryder, Dr. George Bubenik, Dr. Vince Crichton, Dr. David Frazer, Mr. Eugene Mercer, and Mr. Steve Duszinski.

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INTRODUCTION

The moose, *Alces alces* L., is the largest living cervid and readily distinguished by its heavy body, long legs, large ears, short neck and unique dewlap or 'bell' (Herrick 1892; Peterson 1955). This hair-covered fold of skin arises ventrally from the inter-mandibular area and hangs free from the throat region in both sexes (Gunderson and Beer 1953; Burt 1957; Cahalane 1961). The bell can be seen on all four races of moose in North American including *A. a. americana* *A. a. andersoni*, *A. a. shirasi* and *A. a. gigas* (Seton 1929; Peterson 1955; Van Wormer 1972; Franzmann 1978). The bell is also present on *A. a. alces*, *A. a. pfizenmayeri* and *A. a. cameloides* in Europe, central and eastern Siberia and the "Far East" respectively where it is referred to as skjegg or "beard" in Scandinavia (J. Lykke, 7660 Vuku, Norway, personal communication to A. B. Bubenik, Ontario Ministry of Natural Resources, Southern Research Station, Maple, Ontario 1978); Bartzapfen or "cone-like-beard" in German (Zschetzsche 1959); "ear-ring" as translated literally from Russian (Kozhukhov 1965) and "pear with long, hair-like beard" from Chinese (pers. comm.; Peking Zoo, 1978). The distinctive appearance of the bell was even depicted in rock paintings of moose by neolithic hunters in the Lake Baikal area as long ago as three to four thousand years (Vereshchagin 1967) and by North American Indians in rock paintings in the Great Lakes Region (Dewdney and Kidd 1967).

Pendulous structures similar to the bell, but usually less conspicuous, have been described in the neck and head regions of male antelope including the Indian nilgai, *Boselaphus tragocamelus* Blainville, African eland, *Taurotragus* spp. and male goats such as *Capra ibex* L. and *C. hircus* L. (see Grassé 1948; Dorst and Dandelot 1970). The males of several races of domestic goat derived from *C. hircus* carry a varying number of skin appendages on the lower jaw (Darlington 1957) and the beard on old male markhors, *Capra falconeri* L., extends from the chin down the underside of the throat (Drimmer 1954). A dewlap is also seen in male African bovids including the nyala, *Tragelaphus angasi* Gray and the blue wildebeest, *Connochaetes taurinus* (Burchell) (see Dorst and Dandelot 1970). A conspicuous mane is seen along the underside of the neck of male caribou, *Rangifer tarandus caribou* (Gmelin), (see Bergerud 1974) and on both male and female American bison, *Bison bison* L. (see Lott 1974). The Rocky Mountain goat, *Oreamnos americanus* Rafinesque, has a beard of stiff hairs on the underside of the chin in both sexes (Geist 1965).

The African chevrotain, *Hyemoschus aquaticus* (Ogilby), has a glandular area beneath the lower jaw, between the throat and the chin (Dubost 1975). *H. aquaticus* is a tragulid, the group from which modern bovids and cervids are thought to have evolved (Vaughan 1972). White-tailed deer, *Odocoileus virginianus borealis* Miller, have a skin protruberance carrying tactile hairs in this region under the jaw (Bubenik pers. comm. 1977). Lott (1974) quotes Propst (pers. comm. 1971) who observed feral billie goat *Capra* spp. on Catalina Island, California urinating on their beards at certain times of the year. It is possible that the chin gland of the ancestoral tragulids and beards, neck manes and dewlaps may function in some way to produce or broadcast olfactory cues to conspecifics. Certain glands on the head of pronghorn antelope *Antilocapra americana* Ord, (see Kitchen and Bromley 1974), Maxwell's duiker, *Cephalophus maxwelli* (Thünberg), (see Ralls 1969), black-tailed deer, *Odocoileus hemionus columbianus* (Richardson) (see Quay and Müller-Schwarze 1970) and caribou *Rangifer* spp. (see Quay 1955) are thought to play a role in olfactory communication.

The bell seen on moose may function similarly in olfactory communication (Fitzinger 1874; Zschetzche 1959) but 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. Bubenik (pers. comm. 1977) suggested the bell may be a thermoregulatory organ or serve as a visual cue in social interactions aiding to distinguish male, female and immature animals during the antlerless period. Seton (1929) and Bubenik (1973) speculated that the bell in present day moose may be a vestigal organ which through evolution has lost its original function and no longer serves any useful purpose.

The objective of the present study was to determine any morphometric differences in the bells of male and female moose of different ages, to investigate the development, histology and vascularization of the bell and finally to speculate on its possible function.

MATERIALS AND METHODS

The heads of 427 (235 ♂♂, 192 ♀♀) moose killed by hunters and vehicles in the North Central Region of Ontario from 1975-78 were examined. The sample included animals of all ages (some whole fetuses) killed throughout the year but detailed measurements of the bell were taken from only 338 (177 ♂♂, 161 ♀♀) specimens shot during the hunting season (October 4 - December 15) of 1976 and 1977 (Appendix 1). A reference number, sex, date killed and estimated wear class age (Passmore *et al.* 1959) were recorded for each animal. A more precise age for most animals >5 months was later determined by counting cementum rings on central incisors (Sergeant and Pimlott 1959).

Heads, usually severed from the body between the atlas and axis, were placed left side down on a flat sheet of heavy white paper 1 m^2. The hair covering the bell was spread in a normal hanging position. A profile of the bell with hair (WH) was then drawn with a pencil or light felt marker. Four reference points including the angle of the lower jaw, tip of the lower lip, the location of the skin at the distal end of the bell, and tip of the longest hairs hanging from the distal end were included on the drawing (Fig. 1). The hair on the bell was removed by cutting to within 0.5 cm of the skin using heavy-duty electric clippers (Sunbeam clip master model S10A). The head was replaced on the original drawing and the profile of the clipped bell without hair (WOH) was traced. The bell was then cut from the head along the edge of the lower mandibles and examined for external scars,

Fig. 1. Bell of moose drawn in normal hanging position with hair (WH) and without hair (WOH) profile. The four points Ⓧ (A, B, C, D) were used as reference marks. Eight additional arbitrary reference points (▲) facilitated morphometric analysis. These included; jaw length - AB; bell length (WH) - gD; bell length (WOH) - gC; dewlap length (WOH) - go; Tail length (WOH) - oC; hair length - CD; in centimeters and bell area (WH) - AijDeA; bell area (WOH) - AihmlCknfeA; tail area (WOH) - mlCkn; and dewlap area (WOH) - AihmonfeA in square centemeters. Dotted lines indicate the regions from which tissue sections and hair density samples were taken.


i
B
g
A
e
h
o
m
n
f
j
l
k
C
D

folds in the skin, growths or denuded patches and placed in 10% formalin for future reference.

A standard method of numerically computing and comparing bell morphology was established (Fig. 1). Measurements included jaw length (AB), bell length with hair (gD), bell length without hair (gC), bell tail length (oC), hair length (CD), dewlap length (go), area of bell profile with hair (AijDeA), area of bell profile without hair (AihmlCknfeA), area of bell tail without hair (mlCkn) and area of dewlap without hair (AihmonfeA). The junction between dewlap and tail portions of the bell was arbitrarily defined as that point along its length (mm) where the bell was twice its minimum width (lk). Areas were measured from the drawings using an electronic planimeter (Electronic graphics calculator - Numonics Corp. Landsdale Pa. model 276-137). Sample sizes used in subsequent analyses varied to a small extent since all standard measurements could not be taken from every bell.

The rate of hair growth was investigated during the period September 27 - December 30, 1978 using a captive male moose 1.5 years old. Hair at the terminal tip of the bell was clipped to within 2 millimetres of the epidermis on September 27th. Samples of the growing clipped hair were extracted with hair bulbs attached at approximately 2 week intervals to December 30. Control samples of unclipped growing hair in the adjacent tail area were also removed and their lengths compared to clipped samples.

A Duncan's multiple range test (Duncan 1955) was employed for each sex to separate the rank year classes for each of the ten characters measured.

The density of hair along the length of the tail portion of both long and short bells was investigated. Ten bells used for the study were all from 3.5-year-old males and had been stored in formalin. Hair was clipped from 2 skin samples (0.25 cm^2) cut from each of the proximal, mid and distal regions of the tail (Fig. 1). Both the primary and secondary hairs clipped from skin samples were counted in a gridded Syracuse glass using a dissecting microscope.

Moose winter tick, *Dermacentor albipictus*, were counted on the tail portion of 22 male and 32 female bells collected from October 11 to December 15, 1977 and 1976. The tail of the bell without hair was cut transversely into proximal and distal halves. The profile of each half was traced on paper. The area of the profile was measured using an electronic planimeter and the measurement doubled to obtain the total surface area. Each half was digested separately using a 5% solution of sodium hydroxide at 60°C for 24-48 hr. to dissolve hair and soft tissue (Addison *et al.* 1979). The resulting fluid was strained through a 0.5 mm mesh. Ticks were not damaged by the digest treatment. They were washed from the mesh and the various developmental stages counted using a dissecting microscope.

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 paraffin 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. Skin samples from the upper cheek and tarsal gland of a fall killed animal were prepared similarly and compared to bell tissue. Lillies a-b stain (Lillie 1954) and Harris' hematoxylin-eosin were used routinely. Special stains included periodic acid leuco fuchsin or Schiff's reagent (PAS) to identify fungus infection and carbohydrates; Martius yellow-crystal scarlet aniline blue (MSB) to emphasize muscle, keratin and cytoplasm; Verhoeff's Van Giesons (VVG) to identify elastic fibres (Culling 1974) and Alcian green phloxine tartrazine (APT), a variant of the World Health Organization procedure for mixed tumours of the lung (Pers. comm. with Histology department, McKellar General Hospital) to delineate mucin and viral inclusion bodies.

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 gauge 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 taking X-ray photographs. The venous system on several specimens was traced by exposing both anterior sublingual veins and back injecting with blue vinyl acetate. Double injected heads with skin removed, were placed in a 4-10% solution of potasium hydroxide to remove soft tissue and expose a cast of the circulatory system. In addition, a number of selected bells (WOH) 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 X-rayed along with barium injected heads at McKellar General Hospital in Thunder Bay using a Picker 300 MA portable X-ray machine. Dupont chronex 4 film size 14 X 36 inch along with Hi plus screens and a grid were used. Whole heads required an exposure time of 14 seconds at 70 KVP, 15 MA at a 2 metre focal length while X-rays of bell tissue were taken at 60 KVP, 15 MA for 1/2 second.

RESULTS

In order to maximize the number of animals in each age class for analysis, it was desirable to combine data collected in both 1976 and 1977. A meaningful comparison of bell measurements between the two years could only be done with animals in the age classes 0.5 - 4.5 for which there were sufficient moose examined each year. A two-tailed F test (Nie *et al.* 1975) revealed no significant differences in bell measurements (Areas of bell WH, WOH, tail and dewlap and bell tail length) between animals of the same age and sex collected in the two years. The number of animals in older age categories was further increased by grouping 5.5 and 6.5-year-olds, 7.5 to 8.5-year-olds and all animals 9.5 years and older.

The jaw length is used here as an index of the relative size of each animal. It also influences bell measurements directly since the line AB, representing the jaw length on the head tracings, formed a portion of the profile used to calculate the area of the bell (Fig. 1). There were no significant differences between the jaw lengths of males and females of all ages ($P < 0.01$). The jaw length of calves was distinctly shorter than that of older animals (Table 1, Fig. 2). The jaw appears to increase in length in moose up to 3.5 or 4.5 yr but no valid statistical differences were seen in the length of the jaw of animals older than 0.5 yr.

It was suspected that moose hair grows rapidly during the fall and early winter and could substantially influence bell

TABLE 1 Length of lower jaw of moose examined

	Male		Female	
Age (yrs)	N	Mean (cm)*	N	Mean (cm)*
0.5	24	36.8± 3.0 (32.5-45.8)	20	36.5± 3.4 (30.2-45.0)
1.5	51	45.6± 3.1 (37.0-52.5)	47	45.2± 2.8 (37.0-50.0)
2.5	30	47.2± 3.4 (40.6-55.2)	20	45.9± 3.7 (37.4-53.0)
3.5	26	47.3± 3.7 (40.0-54.0)	10	48.4± 2.3 (46.0-52.0)
4.5	7	49.4± 2.9 (46.5-54.0)	12	48.7± 3.0 (45.0-53.5)
(5.5-6.5)	18	48.3± 2.4 (43.0-51.0)	15	49.5± 2.6 (44.5-53.8)
(7.5-8.5)	3	45.1± 6.8 (37.6-50.7)	8	47.8± 2.8 (44.0-53.0)
9.5+	8	47.7± 2.2 (43.5-51.0)	18	48.6± 2.3 (44.5-53.8)

* Mean, ± S. D. (range)

ANOVA (1 way) - Between age classes

♂♂ Jaw length F = 31.52 Range Test

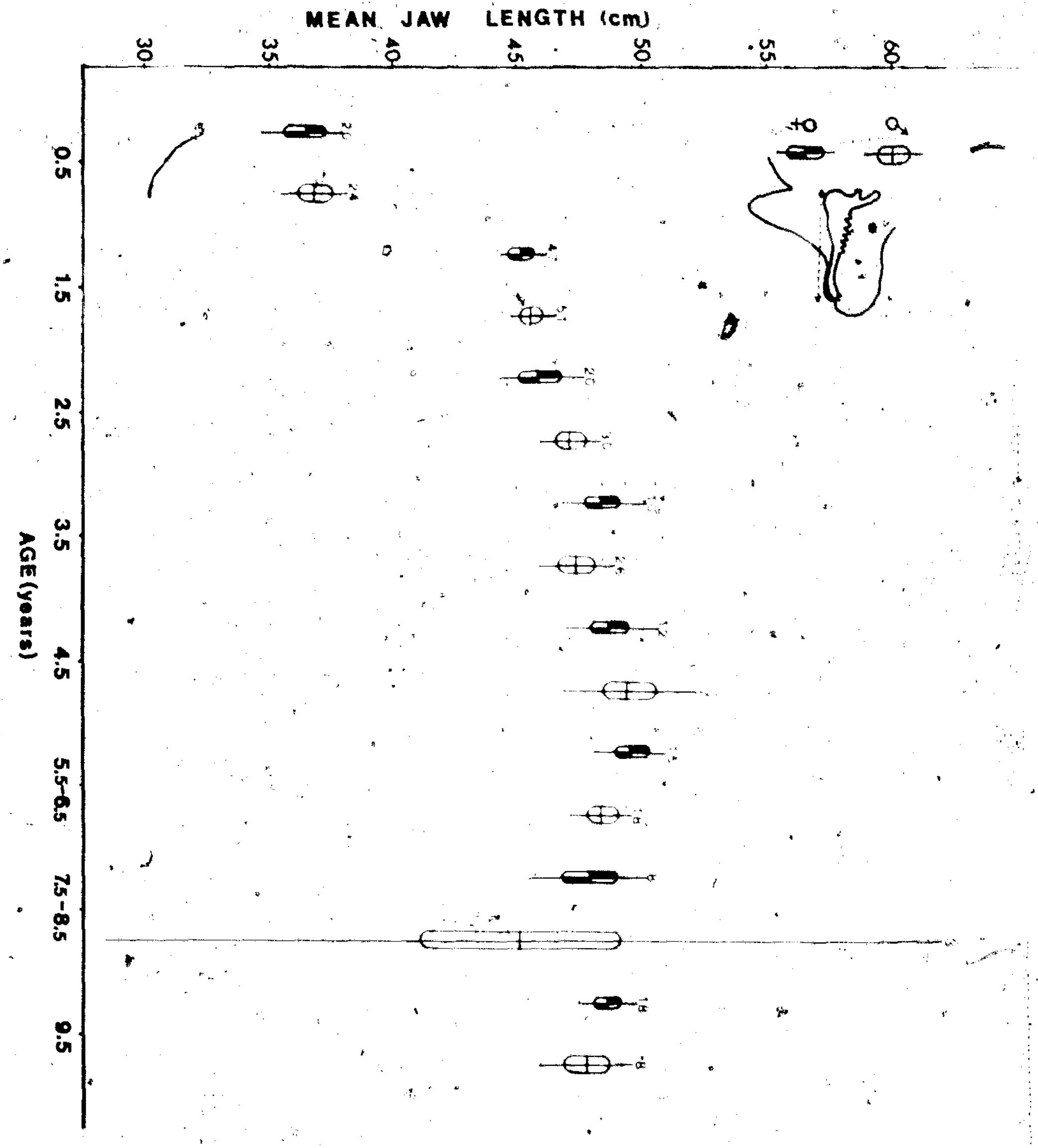
0.5 (7.5-8.5) 1.5 2.5 3.5 9.5+ (5.5-6.5) 4.5

♀♀ Jaw length F = 37.95 Range test

0.5 1.5 2.5 (7.5-8.5) 3.5 9.5+ 4.5 (5.5-6.5)

Note: Mean values for age classes arranged in ascending order of magnitude. Age classes not underscored by the same line are significantly different ($P < 0.05$).

Fig. 2. Length of the lower jaw of moose in relation to sex and age. The horizontal bar indicates means; vertical bars, 95% confidence limits; vertical bar enclosed by curve, one standard error above and below the mean. Sample sizes are indicated for each age group.


MEAN JAW LENGTH (cm)
30
35
40
45
50
55
60
♀
♂
AGE (years)
0.5
1.5
2.5
3.5
4.5
5.5-6.5
7.5-8.5
9.5

measurements. The rate of hair growth at the end of the bell was examined on a 1.5-year-old captive male. The mean increase in length of clipped and unclipped hair during the 94 day period was 4.3 cm. (Fig. 3). However, the hair grew 2.8 cm. from October 4 to November 6, the period in which 77 percent of the bells were collected in 1976 and 1977.

To determine if the hair growth during the collection period influenced bell measurements taken from head tracings, the length of hair and area of bell with hair from animals taken early in the hunting season (October 4 - November 6) were compared with those taken later (November 7 - December 15). Subsamples from 1976 and 1977 for this comparison were of sufficient size (≥ 4) in only 4 age groups (0.5, 1.5, 2.5, 3.5); females; 0.5 yr, from 1976 (N=3) were excluded. The length of the hair as measured from the tracings did differ significantly ($P < 0.5$) between early and late male calves in both 1976 and 1977, male yearlings in 1976 and female yearlings in both 1976 and 1977. The bell hair on animals killed late in the season were 5 - 50 percent longer than hair on animals killed early. There was no difference in the hair length between early and late female calves or male yearlings taken in 1977. These analyses also demonstrated that the mean length of the hair on the tip of the bell was similar in males and females of all ages tested (Table 2). A significant difference ($P < 0.05$) in the area of the bell with hair was only seen between early and late male calves of both 1976 and 1977 (up to 50% increase), but not in female calves, although sample sizes were small.

Fig. 3. Length of clipped and unclipped hair sampled from the tip of the bell tail of a 1.5 yr-old captive male moose at intervals from 27 September - 30 December, 1978. Vertical lines subtending sample size indicate range of hair measurement; horizontal lines indicate means. A = difference in mean hair length between 4 October and 30 December. B = difference in mean hair length 27 September and 30 December.

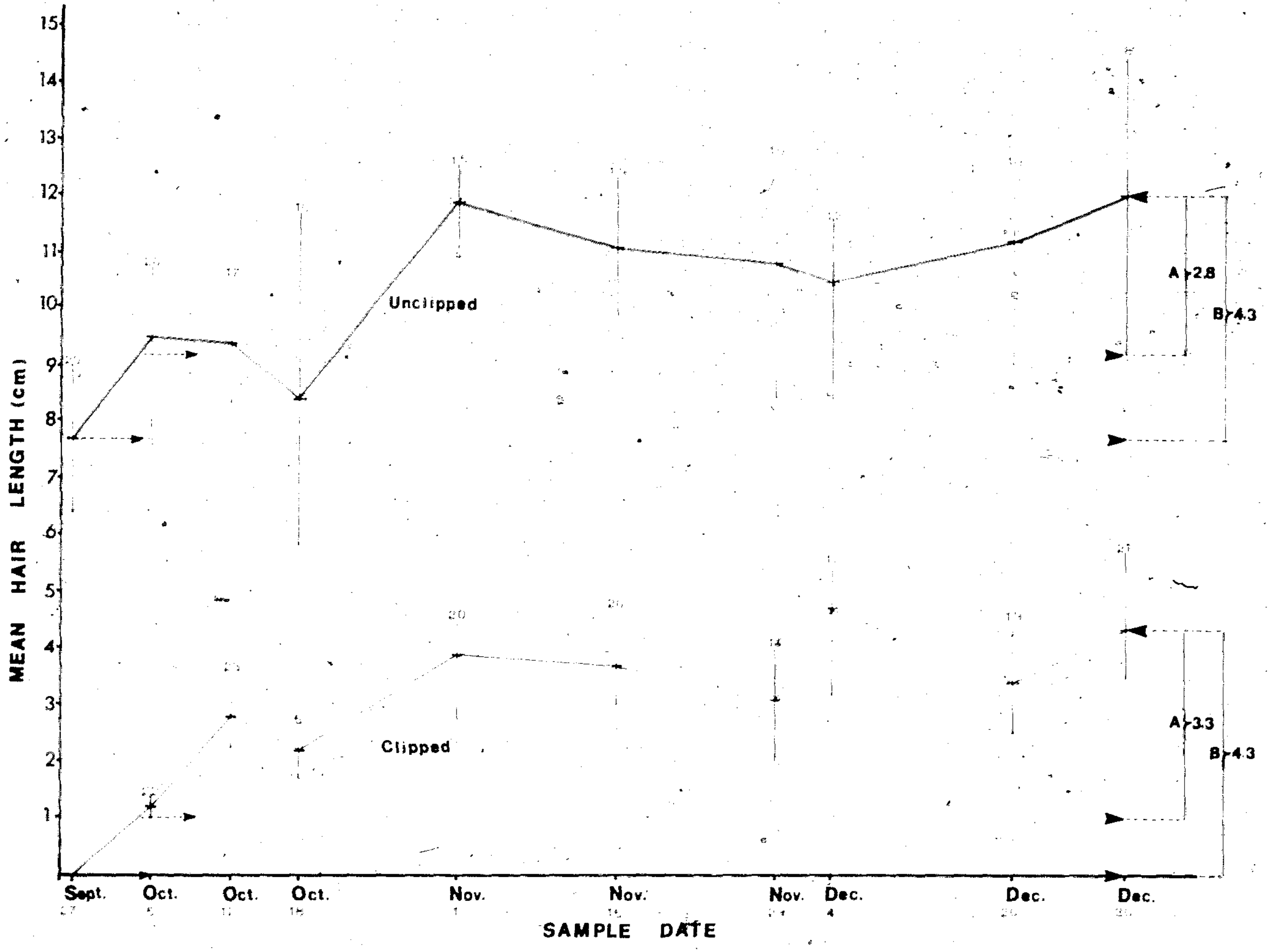

MEAN HAIR LENGTH (cm)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Unclipped
Clipped
A 2.8
B 4.3
A 3.3
B 4.3
Sept.
Oct.
5
Oct.
Oct.
Nov.
1
Nov.
Nov.
Dec.
4
Dec.
Dec.
SAMPLE DATE
20
20
14

TABLE 2 . Length of hair at the distal end of the moose bell

Age (yrs)	Male N	Male Mean (cm)*	Female N	Female Mean (cm)*
0.5	23	6.1± 1.6 (3.5- 9.3)	20	6.5± 1.8 (2.5-10.7)
1.5	52	7.0± 1.9 (1.9-10.6)	48	7.4± 1.8 (3.0-11.8)
2.5	30	8.0± 1.9 (4.0-11.5)	19	6.6± 1.8 (3.8-10.6)
3.5	25	7.2± 1.8 (4.1-11.2)	10	8.0± 2.5 (3.1-12.0)
4.5	6	8.2± 1.3 (6.5-10.0)	11	7.1± 1.0 (5.6- 9.1)
(5.5-6.5)	17	7.7± 1.6 (5.0-10.2)	15	7.3± 2.5 (3.0-12.2)
(7.5-8.5)	4	7.6± 2.1 (5.3-10.3)	9	8.0± 1.1 (6.2- 9.6)
9.5+	8	7.3± 1.5 (5.1- 9.2)	19	7.8± 2.5 (3.0-12.0)

* Mean, ± S. D. (range)

ANOVA (1 way) - Between age classes

♂♂ Hair length F = 2.76 Range Test

0.5 1.5 3.5 9.5+ (7.5-8.5) (5.5-6.5) 2.5 4.5

♀♀ Hair length F = 1.38 Range test

0.5 2.5 4.5 (5.5-6.5) 1.5 9.5+ 3.5 (7.5-8.5)

Note: Mean values for age classes arranged in ascending order of magnitude. Age classes not underscored by the same line are significantly different ($P < 0.05$).

It is recognized that both increase in size of moose and seasonal growth of hair during the collection period influenced bell measurements. The effect was undoubtedly greatest in calves yet the mean bell measurements of calves still remained distinct from other age groups. An arbitrary decision was made therefore, to ignore these increases in bell measurements during subsequent analysis of data.

The bell of male moose was significantly longer ($P < 0.05$) than female bells except on animals older than 6.5 yr. (Tables 3 and 4, Figs. 4 and 5). The longest bell measured was 66.5 cm from a 3.5-year-old male. The longest bell on a female was 40.8 cm from a 12.5-year-old animal. The bell was progressively longer on males up to 4.5 yr but was shorter in older males. The tail portion of the bell became progressively longer on males and females up to 3.5 yr but was shorter in older males and changed little in length on older females (Table 5, Fig. 6). The dewlap portion of the bell changed little in depth on females ≥ 3.5 yr (Table 6, Fig. 7) but increased significantly in males ≥ 7.5 yr.

The profile area of the male bell measured both with hair and without hair was greater than the area of female bells in all age groups (Tables 7 and 8, Fig. 8). The area of male bells increased with age, being greatest in older animals. The area of the dewlap portion of male bells also increased with age but the area of the tail decreased in males older than 3.5 yr (Tables 9 and 10, Figs. 9 and 10). The area of the bell increased on females up to 3.5 yr. and showed little futher change in older animals.

TABLE 3 Length of the entire moose bell with hair

	Male		Female	
Age (yrs)	N	Mean (cm)*	N	Mean (cm)*
0.5	24	23.1 ± 4.2 (15.7-33.4)	20	21.2 ± 3.0 (14.5-26.0)
1.5	51	32.4 ± 6.1 (20.2-49.2)	47	24.6 ± 4.5 (15.4-33.0)
2.5	29	34.8 ± 7.1 (18.0-51.5)	20	26.8 ± 4.3 (20.2-34.0)
3.5	25	38.9 ± 8.8 (22.9-66.5)	10	30.4 ± 5.6 (19.0-38.7)
4.5	7	42.1 ± 8.0 (32.6-56.7)	11	28.3 ± 3.4 (22.0-34.5)
(5.5-6.5)	18	35.8 ± 7.2 (22.6-47.0)	15	28.5 ± 4.6 (21.0-37.4)
(7.5-8.5)	3	34.8 ± 11.0 (27.0-47.3)	8	27.3 ± 3.8 (22.9-34.7)
9.5+	8	32.7 ± 5.1 (24.5-41.0)	18	30.0 ± 6.7 (16.2-40.8)

* Mean, ± S. D. (range)

ANOVA (1 way) - Between age classes

♂♂ Bell length F = 12.45 Range Test

0.5 1.5 9.5+ (7.5-8.5) 2.5 (5.5-6.5) 3.5 4.5

♀♀ Bell length F = 8.21 Range test

0.5 1.5 2.5 (7.5-8.5) 4.5 (5.5-6.5) 9.5+ 3.5

Note: Mean values for age classes arranged in ascending order of magnitude. Age classes not underscored by the same line are significantly different ($P < 0.05$).

TABLE 4 Length of the entire moose bell measured without hair

	Male		Female	
Age (yrs)	N	Mean (cm)*	N	Mean (cm)*
0.5	23	17.1 ± 3.8 (10.2-25.2)	20	14.7 ± 2.5 (10.0-20.1)
1.5	51	25.4 ± 6.2 (12.0-41.2)	47	17.3 ± 4.4 (8.7-26.5)
2.5	29	27.8 ± 6.7 (10.5-41.9)	19	20.3 ± 4.3 (13.0-26.6)
3.5	26	32.0 ± 9.0 (17.7-60.7)	10	22.4 ± 4.6 (14.0-29.3)
4.5	6	31.5 ± 6.3 (22.6-40.8)	12	21.5 ± 2.9 (15.7-25.4)
(5.5-6.5)	18	27.6 ± 7.5 (16.3-42.0)	15	21.2 ± 3.3 (16.3-27.0)
(7.5-8.5)	3	26.9 ± 9.1 (19.0-37.0)	8	19.2 ± 4.0 (14.4-26.5)
9.5+	8	25.4 ± 5.8 (15.5-34.3)	18	22.4 ± 5.8 (13.2-32.0)

* Mean, ± S. D. (range)

ANOVA (1 way) - Between age classes

♂♂ Bell length F = 9.70 Range Test

0.5 9.5+ 1.5 (7.5-8.5) (5.5-6.5) 2.5 4.5 3.5

♀♀ Bell length F = 8.28 Range test

0.5 1.5 (7.5-8.5) 2.5 (5.5-6.5) 4.5 9.5+ 3.5

Note: Mean values for age classes arranged in ascending order of magnitude. Age classes not underscored by the same line are significantly different ($P < 0.05$).

Fig. 4. Length of entire moose bell with hair (WH) in relation to sex and age. Vertical lines subtending sample size indicate 95% confidence limits; horizontal line indicate mean; vertical lines enclosed by curve indicate one standard error above and below the mean.

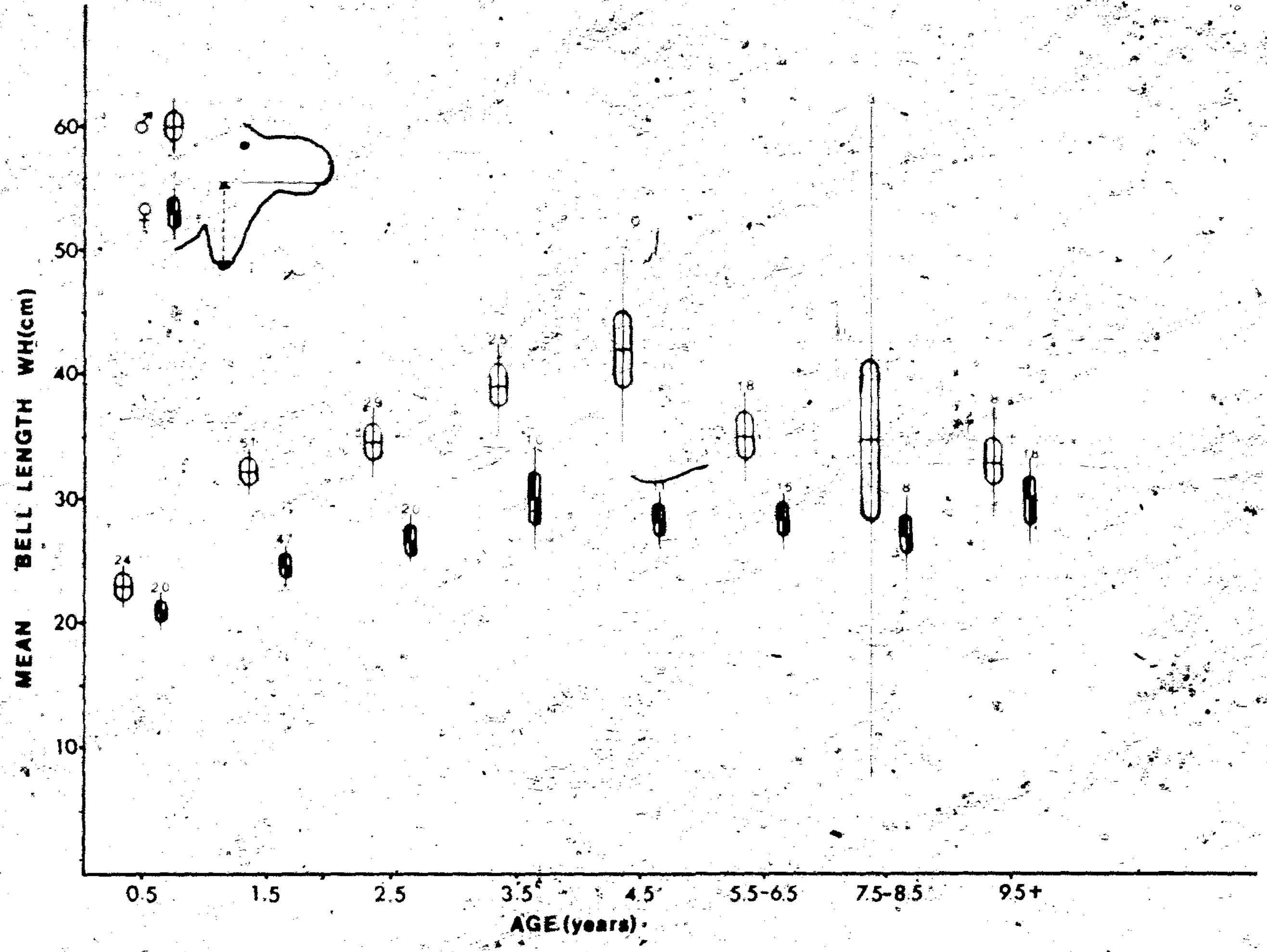

MEAN BELL LENGTH WH(cm)
10
20
30
40
50
60
♂
♀
24
20
51
47
29
20
25
10
18
15
8
8
18
0.5
1.5
2.5
3.5
4.5
5.5-6.5
7.5-8.5
9.5+
AGE (years)

Fig. 5. Length of entire moose bell without hair (WOH) in relation to sex and age. Vertical lines subtending sample sizes indicate 95% confidence limits; horizontal lines indicate means; vertical lines enclosed by curve indicate one standard error above and below the mean.

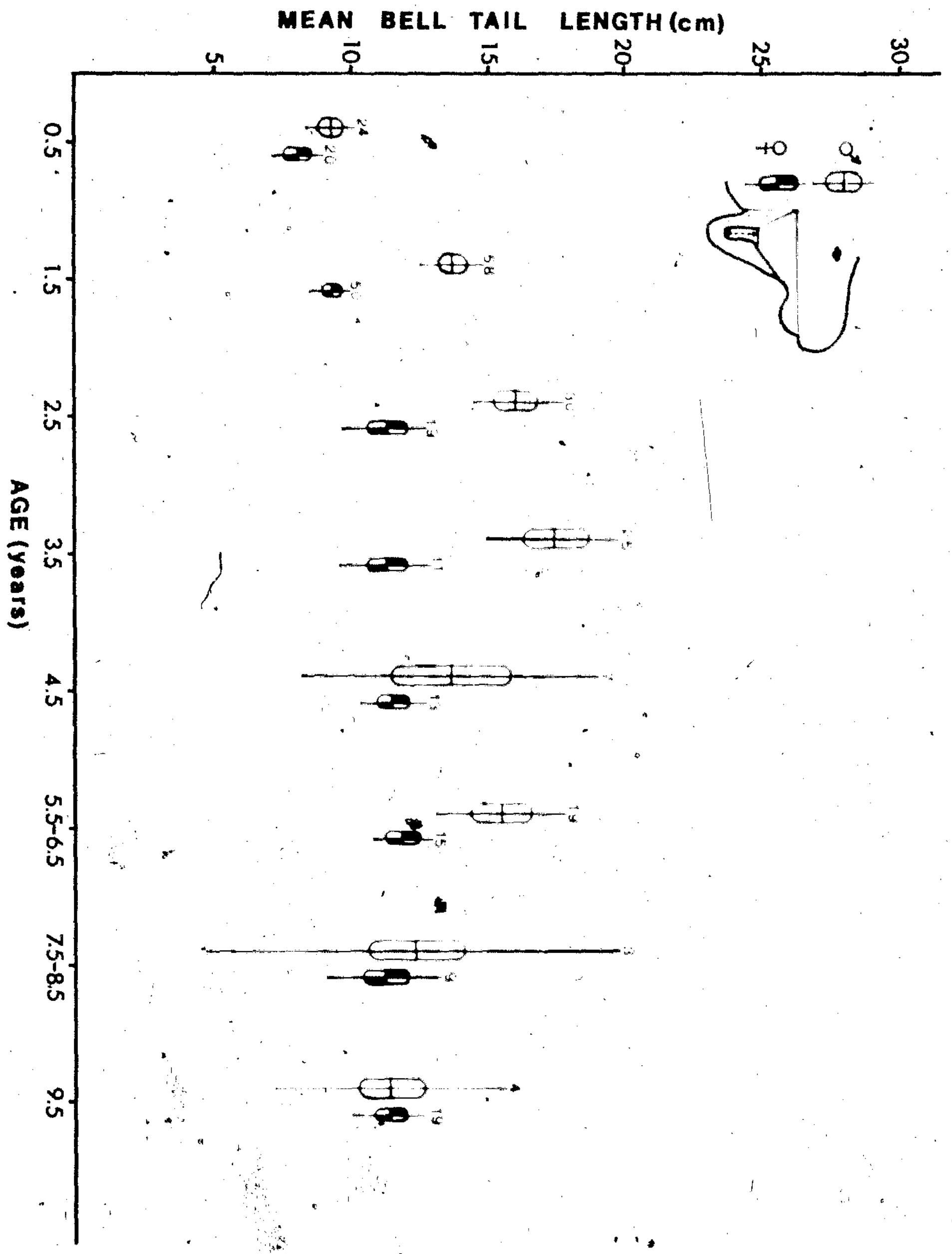

MEAN BELL TAIL LENGTH (cm)
5
10
15
20
25
30
AGE (years)
0.5
1.5
2.5
3.5
4.5
5.5-6.5
7.5-8.5
9.5
♂
♀
24
20
58
50
13
15
19

TABLE 5 Length of the tail portion of the moose bell measured without hair

	Male		Female	
Age (yrs)	N	Mean (cm)*	N	Mean (cm)*
0.5	24	9.3± 2.2 (5.5-12.9)	20	8.1± 1.9 (5.3-13.4)
1.5	58	13.7± 4.2 (6.3-26.0)	50	9.3± 2.5 (4.5-14.3)
2.5	30	16.1± 4.5 (5.9-25.5)	19	11.3± 3.1 (5.8-17.5)
3.5	25	17.5± 5.9 (6.2-36.5)	11	11.3± 2.6 (6.9-16.1)
4.5	7	13.7± 5.9 (3.2-20.2)	13	11.5± 1.9 (8.4-14.4)
(5.5-6.5)	19	15.5± 4.9 (5.6-22.2)	15	11.9± 2.1 (8.5-15.5)
(7.5-8.5)	3	12.3± 3.0 (9.0-15.0)	9	11.3± 2.6 (7.2-16.2)
9.5+	4	11.4± 2.7 (9.1-14.8)	19	11.4± 2.9 (7.0-18.2)

* Mean, ± S. D. (range)

ANOVA (1 way) - Between age classes

♂♂ Tail length F = 7.67 Range Test

0.5 9.5 (7.5-8.5) 4.5 1.5 (5.5-6.5) 2.5 3.5

♀♀ Tail length F = 6.05 Range test

0.5 1.5 (7.5-8.5) 3.5 2.5 9.5+ 4.5 (5.5-6.5)

Note: Mean values for age classes arranged in ascending order of magnitude. Age classes not underscored by the same line are significantly different ($P < 0.05$).

Fig. 6. Length of the bell tail without hair (WOH) in relation to sex and age of moose. Vertical lines subtending sample sizes indicate 95% confidence limits; horizontal lines indicate means; vertical lines enclosed by curve indicate one standard error above and below the mean.

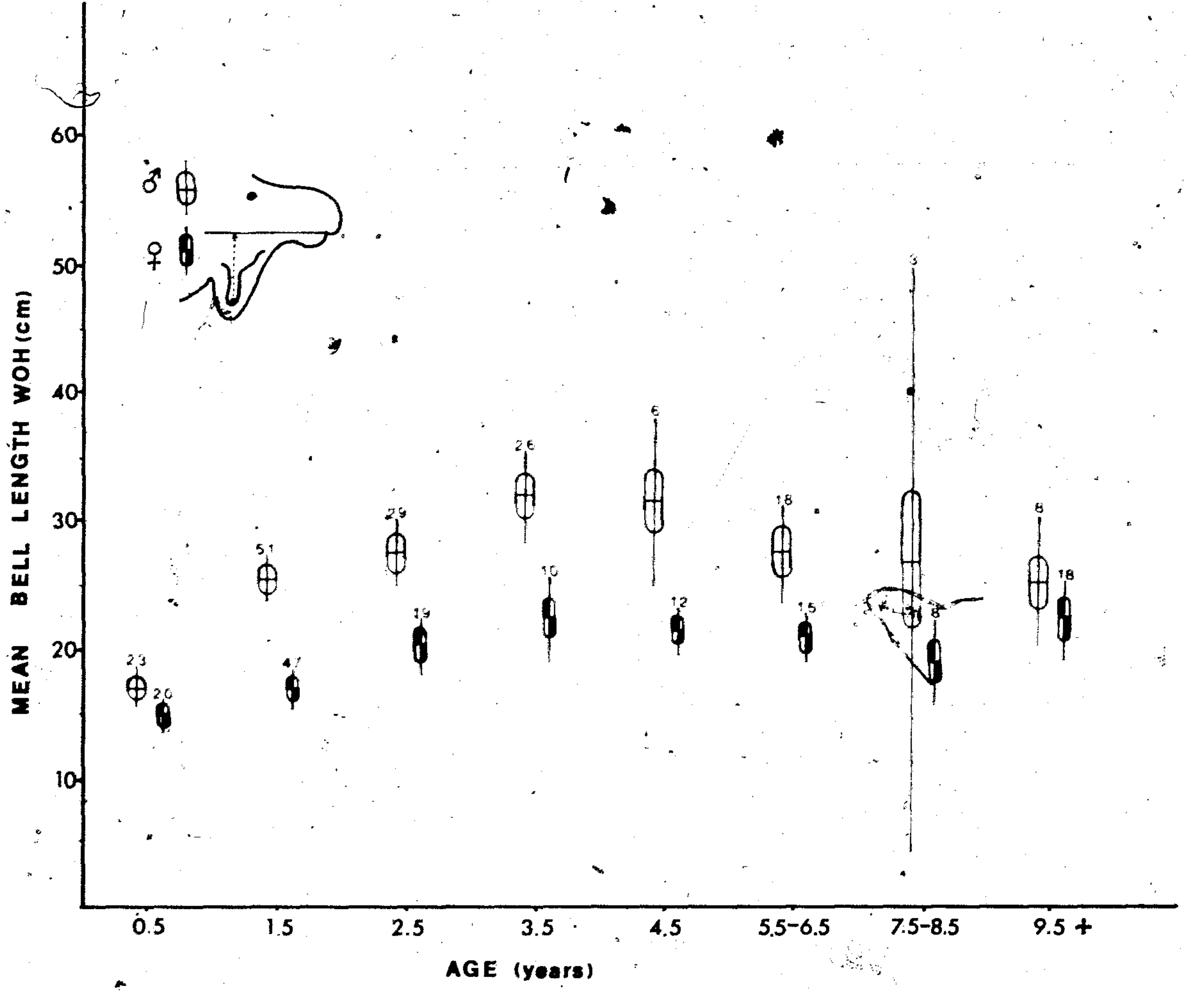

MEAN BELL LENGTH WOH (cm)
10
20
30
40
50
60
♂
♀
23
20
51
47
29
19
26
10
6
12
18
15
8
8
18
0.5
1.5
2.5
3.5
4.5
5.5-6.5
7.5-8.5
9.5 +
AGE (years)

TABLE 6 Length of the dewlap portion of the moose bell measured without hair

	Male		Female	
Age (yrs)	N	Mean (cm)*	N	Mean (cm)*
0.5	23	7.7± 2.6 (3.6-12.5)	20	6.5± 2.1 (3.1-10.2)
1.5	51	11.6± 4.0 (3.5-18.8)	47	8.0± 3.2 (1.4-17.2)
2.5	29	12.2± 4.6 (3.8-22.8)	19	9.0± 2.7 (5.3-13.7)
3.5	26	15.2± 4.7 (6.1-24.5)	10	11.0± 2.4 (7.1-14.0)
4.5	6	16.1± 4.4 (12.7-24.1)	12	9.7± 2.2 (5.9-12.0)
(5.5-6.5)	18	13.2± 5.4 (5.5-24.0)	15	9.3± 2.3 (5.5-14.7)
(7.5-8.5)	3	22.6± 3.2 (19.0-24.7)	8	8.1± 2.3 (5.2-10.5)
9.5	8	19.7± 5.9 (10.4-30.0)	18	11.8± 4.8 (4.0-23.5)

* Mean, ± S. D. (range)

ANOVA (1 way) - Between age classes

♂♂ Dewlap length F = 11.9 Range Test

0.5 1.5 2.5 (5,5-6.5) 3.5 4.5 9.5+ (7.5-8.5)

♀♀ Dewlap length F = 5.6 Range test

0.5 1.5 (7.5-8.5) 2.5 (5.5-6.5) 4.5 3.5 9.5+

Note: Mean values for age classes arranged in ascending order of magnitude. Age classes not underscored by the same line are significantly different ($P<0.05$).

Fig. 7. Length of dewlap portion of the bell without hair (WOH) in relation to sex and age of moose. Vertical lines subtending sample sizes indicate 95% confidence limits; horizontal lines indicate means; vertical lines enclosed by curve indicate one standard error above and below the mean.

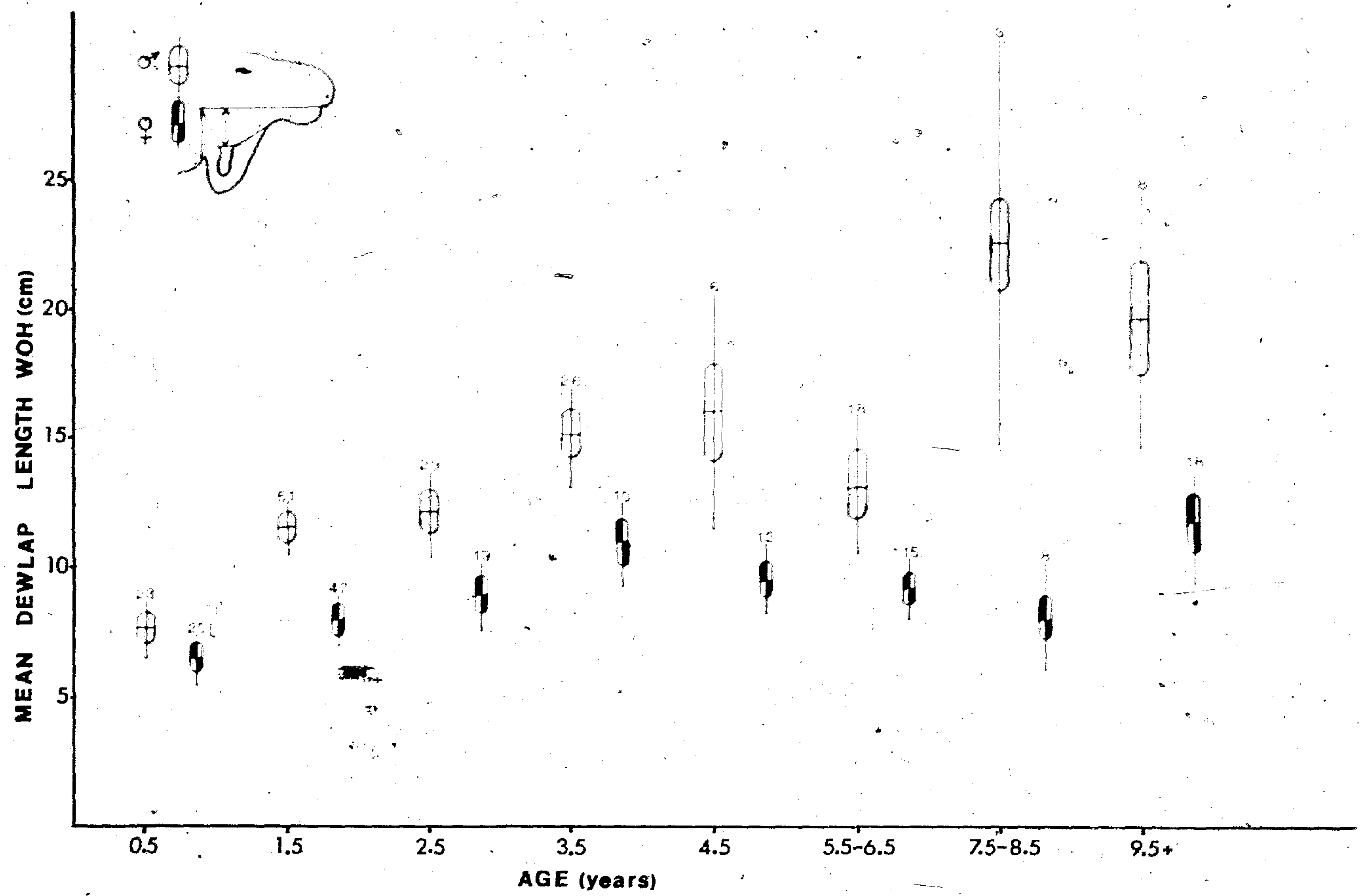

♂
♀
MEAN DEWLAP LENGTH WOH (cm)
5
10
15
20
25
0.5
1.5
2.5
3.5
4.5
5.5-6.5
7.5-8.5
9.5+
AGE (years)

TABLE 7 Profile area of the entire moose bell with hair

	Male		Female	
Age (yrs)	N	Me[illegible]cm)*	N	Mean (cm)*
0.5	24	439±126 (215-716)	20	401±100 (258-611)
1.5	51	662±146 (331-971)	47	541±124 (306-795)
2.5	29	699±193 (324-983)	20	589±152 (367-903)
3.5	25	803±191 (473-1146)	10	700±187 (403-1006)
4.5	7	830±143 (661-1041)	11	626±148 (442-843)
(5.5-6.5)	18	783±171 (543-1085)	15	617±162 (342-935)
(7.5-8.5)	3	1039±185 (904-1249)	8	648±146 (460-897)
9.5+	8	834±134 (661-981)	18	652±177 (226-939)

* Mean, ± S. D. (range)

ANOVA (1 way) - Between age classes

♂♂ Profile area F = 14.74 Range Test

0.5 1.5 2.5 (5.5-6.5) 3.5 4.5 9.5+ (7.5-8.5)

♀♀ Profile area F = 7.08 Range test

0.5 1.5 2.5 (5.5-6.5) 4.5 (7.5-8.5) 9.5+ 3.5

Note: Mean values for age classes arranged in ascending order of magnitude. Age classes not underscored by the same line are significantly different ($P < 0.05$).

TABLE 8 Profile area of the moose bell measured without hair

Age (yrs)	Male N	Male Mean (cm)*	Female N	Female Mean (cm)*
0.5	23	225± 58 (131-349)	20	203± 53 (115-280)
1.5	51	337±102 (115-585)	47	278± 79 (98-433)
2.5	29	357±119 (161-582)	19	302± 84 (156-448)
3.5	26	432±111 (184-643)	10	345± 77 (224-487)
4.5	6	417± 76 (332-526)	12	332±105 (215-522)
(5.5-6.5)	18	397±109 (165-627)	15	304± 79 (165-454)
(7.5-8.5)	3	599± 60 (545-664)	8	307± 86 (184-420)
9.5+	8	499±104 (402-692)	18	356±110 (138-544)

* Mean, ± S. D. (range)

ANOVA (1 way) - Between age classes

♂♂ Profile area F = 13.16 Range Test

0.5 1.5 2.5 (5.5-6.5) 4.5 3.5 9.5+ (7.5-8.5)

♀♀ Profile area F = 6.03 Range test

0.5 1.5 2.5 (5.5-6.5) (7.5-8.5) 4.5 3.5 9.5+

Note: Mean values for age classes arranged in ascending order of magnitude. Age classes not underscored by the same line are significantly different ($P<0.05$).

Fig. 8. Profile area of the entire bell with hair (WH) and without hair (WOH) in relation to sex and age of moose. Vertical lines subtending sample sizes indicate 95% confidence limits; horizontal lines indicate means; vertical lines enclosed by curve indicate one standard error above and below the mean.

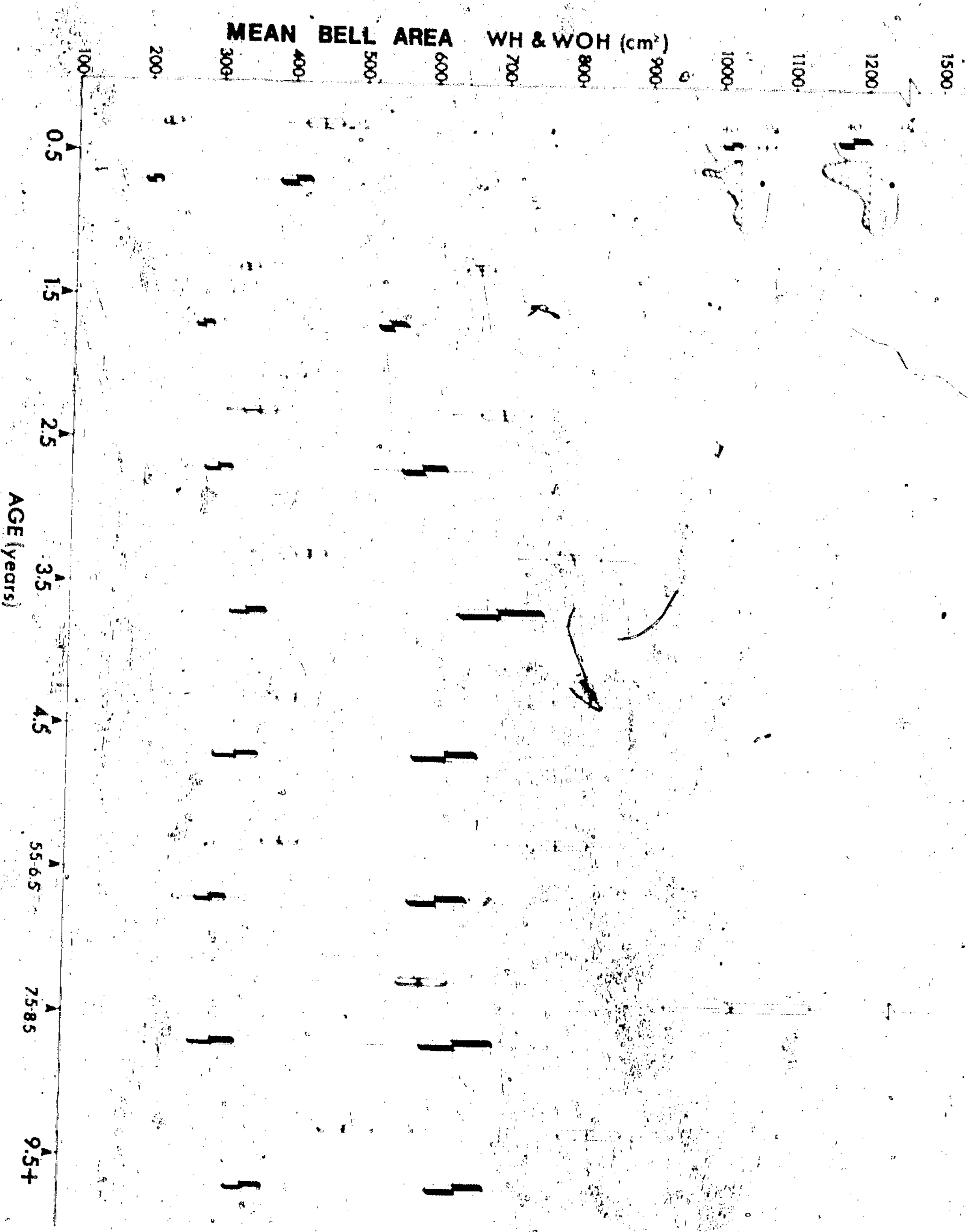

MEAN BELL AREA WH & WOH (cm²)
100
200
300
400
500
600
700
800
900
1000
1100
1200
1500
AGE (years)
0.5
1.5
2.5
3.5
4.5
55-6.5
7.5-8.5
9.5+

TABLE 9 Profile area of the dewlap portion of the moose bell measured without hair

	Male		Female	
Age (yrs)	N	Mean (cm)*	N	Mean (cm)*
0.5	23	204± 57 (110-323)	19	175± 55 (92-268)
1.5	53	301± 99 (85-534)	48	258± 80 (80-413)
2.5	28	308±117 (106-543)	19	277± 84 (133-418)
3.5	26	390±110 (141-602)	10	316± 74 (205-461)
4.5	6	374±113 (296-482)	11	308±109 (184-497)
(5.5-6.5)	18	360±113 (139-594)	15	277± 78 (139-435)
(7.5-8.5)	3	585± 40 (545-624)	8	278± 84 (164-379)
9.5+	8	481±108 (375-692)	17	319±102 (117-505)

* Mean, ± S. D. (range)

ANOVA (1 way) - Between age classes

♂♂ Profile area F = 13.1 Range Test

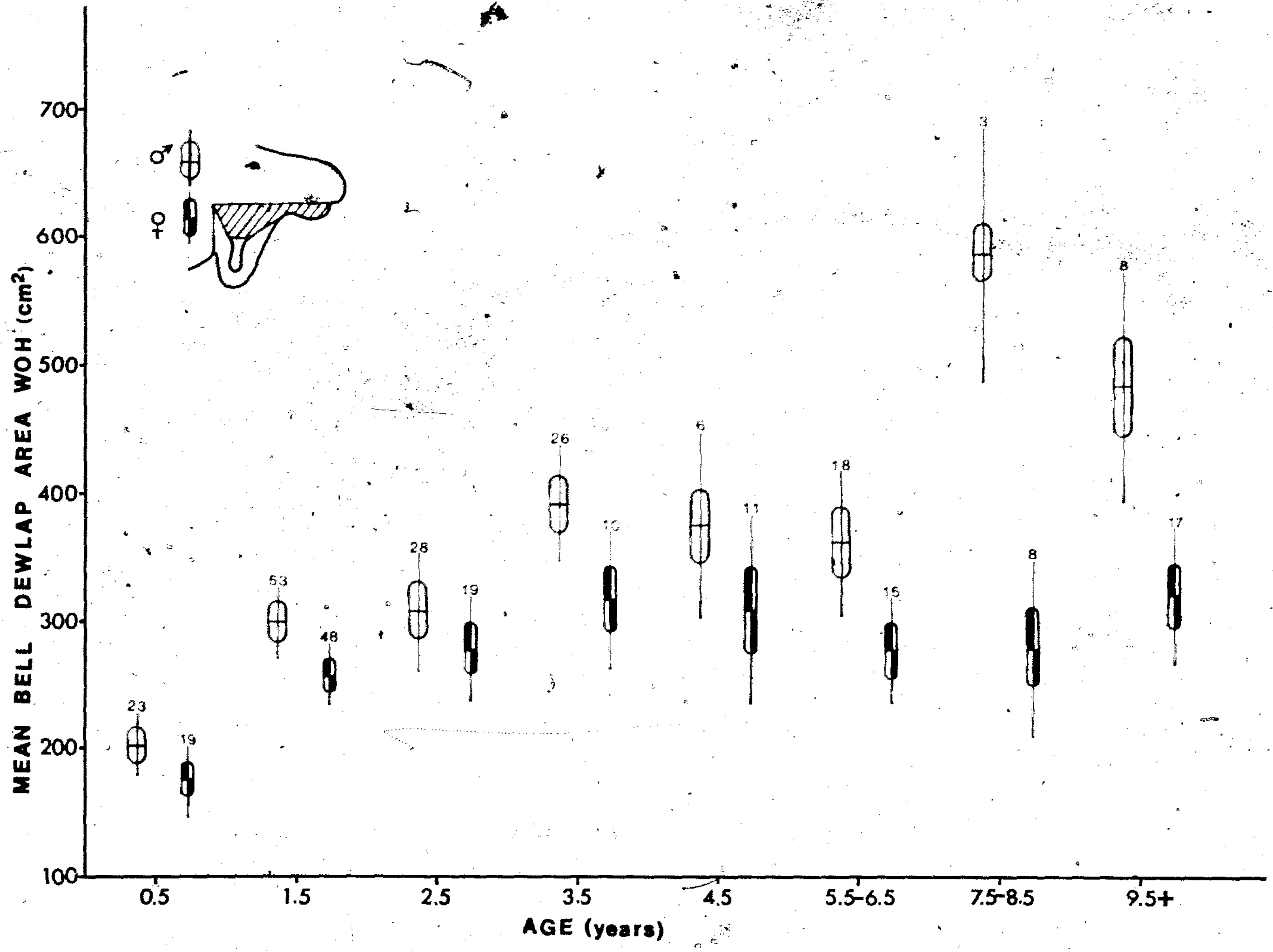
0.5 1.5 2.5 (5.5-6.5) 4.5 3.5 9.5+ (7.5-8.5)

♀♀ Profile area F = 5.35 Range test

0.5 1.5 (5.5-6.5) 2.5 (7.5-8.5) 4.5 3.5 9.5+

Note: Mean values for age classes arranged in ascending order of magnitude. Age classes not underscored by the same line are significantly different ($P < 0.05$).

Fig. 9. Profile area of the dewlap portion of the bell without hair (WOH) in relation to sex and age of moose. Vertical lines subtending sample sizes indicate 95% confidence limits; horizontal lines indicate means; vertical lines enclosed by curve indicate one standard error above and below the mean.



MEAN BELL DEWLAP AREA WOH (cm²)
700
600
500
400
300
200
100
♂
♀
23
19
53
48
28
19
26
10
6
11
18
15
3
8
8
17
0.5
1.5
2.5
3.5
4.5
5.5–6.5
7.5–8.5
9.5+
AGE (years)

TABLE 10 Profile area of the tail portion of the moose bell measured without hair

	Male		Female	
Age (yrs)	N	Mean (cm)*	N	Mean (cm)*
0.5	24	21.6± 5.2 (10.7-31.4)	19	18.4± 5.1 (7.9-31.4)
1.5	58	36.3±12.5 (11.2-72.4)	50	22.0± 6.7 (7.5-39.8)
2.5	30	43.9±13.3 (15.5-67.5)	19	26.4± 6.7 (10.6-37.6)
3.5	25	43.9±13.9 (18.7-82.2)	11	28.5± 5.6 (19.3-36.9)
4.5	7	39.5±17.3 (15.0-68.9)	13	26.5± 4.9 (18.7-35.1)
(5.5-6.5)	19	38.8±11.5 (14.9-57.0)	15	26.6± 6.5 (18.9-40.4)
(7.5-8.5)	3	24.6±11.9 (15.0-38.0)	9	28.8± 6.8 (19.7-40.7)
9.5+	4	31.1±12.9 (14.8-44.4)	19	27.1± 8.1 (14.2-42.5)

* Mean, ± S. D. (range)

ANOVA (1 way) - Between age classes

♂♂ Profile area F = 8.56 Range Test

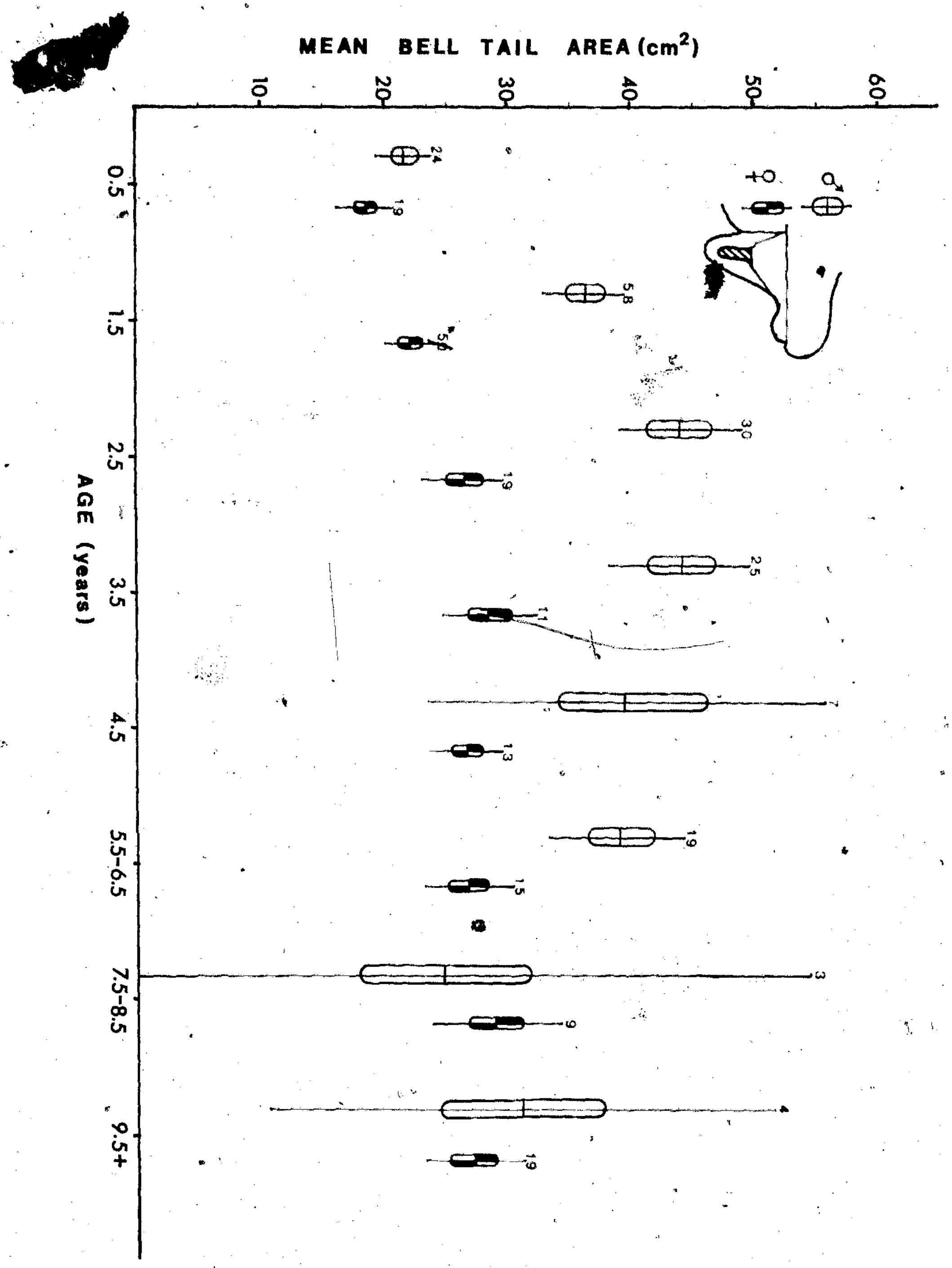
0.5 (7.5-8.5) 9.5+ 1.5 (5.5-6.5) 4.5 3.5 2.5

♀♀ Profile area F = 5.65 Range test

0.5 1.5 2.5 4.5 (5.5-6.5) 9.5+ 3.5 (7.5-8.5)

Note: Mean values for age classes arranged in ascending order of magnitude. Age classes not underscored by the same line are significantly different ($P < 0.05$).

Fig. 10. Profile area of the tail portion of the bell without hair (WOH) in relation to sex and age of moose. Vertical lines subtending sample sizes indicate 95% confidence limits; horizontal lines indicate means; vertical lines enclosed by curve indicate one standard error above and below the mean.


MEAN BELL TAIL AREA (cm²)
10
20
30
40
50
60
AGE (years)
0.5
1.5
2.5
3.5
4.5
5.5-6.5
7.5-8.5
9.5+
♂
♀
24
19
58
56
30
19
25
11
7
13
19
15
3
9
4
19

A summary of significant morphometric differences between the bells of male and female moose of all ages is shown in Table 11. Drawings in Appendix 2 illustrate the typical morphology of bells on animals of various ages. Appendix 3 shows bell profiles drawn with and without hair from selected animals.

A single scar was found on the distal tip of some bells (Figs. 11 and 12). Scars were devoid of hair and appeared as a slightly raised ridge of hardened tissue, 5-35 mm long ($\bar{X} = 13.7 \pm 6.8$) and 2-10 mm wide ($\bar{X} = 4.3 \pm 3.0$). A terminal scar was found on 14.5% of male bells examined and on a 2.6% of females but was not seen on calves or yearlings (Table 12). Males $\gtrsim$ 5.5 yr showed a higher incidence (52%) of a terminal scar than females (2%) of similar age. Bells with a terminal scar had a significantly shorter tail ($P < 0.05$) than those without a scar with the exception of one fairly long scarred female bell (Table 12). Sack or bladelike bells comprised of a broad dewlap with a ventral scar, but no tail, appear to be nearly exclusively a male phenomenon (Table 13). Only one female (12.5 yr) in a total of 156 fall specimens examined, had completely lost its tail. Conversely 8 of 179 males (4.5%) aged 2.5 to 10.5 yr had a sack-like bell without a tail. (Appendix 3). Eight additional sack-like bells from males 2.5 - 15.5 yr were examined incidentally during the study (Table 13). Each had a terminal scar and no tail.

Histologically, scars consisted of glassy, elongated collagen fibres orientated at right angles to fibres in the adjacent undamaged

TABLE 11 Summary of morphometric differences in the bell of male and female moose

Character measured (cm, cm^2)	Age (yrs)							
	0.5	1.5	2.5	3.5	4.5	(5.5-6.5)	(7.5-8.5)	9.5^+
Jaw length	-	-	-	-	-	-	-	-
Bell length (WH)	-	X[1,2]	X	X	X	X	-	-
Bell length (WOH)	X	X	X	X	X	X	-	-
Bell tail length	-	X	X	X	-	X	-	-
Bell dewlap length	-	X	X	X	X	X	X	X
Bell hair length	-	-	X	-	-	-	-	-
Bell area (WH)	-	X	X	-	X	X	X	X
Bell area (WOH)	-	X	-	X	-	X	X	X
Bell tail area	X	X	X	X	X	X	-	-
Bell dewlap area	-	X	-	-	-	X	X	X

1. X indicates significant differences ($P<0.05$- 't' test) between means (♂>♀)

2. Sample sizes (N) tested are listed in Tables 1 to 10.

Fig. 11. Scar (15 X 4 mm) on the ventral edge of a sack-type bell from a 15.5 yr-old male moose with no apparent bell tail. The injected vascular system of this bell is shown in Fig. 22.

Fig. 12. Scar on the distal tip of a clipped tail-type bell from a 6.5 yr-old male moose.

Fig. 13. Longitudinal section of scar tissue at the distal tip of the bell tail of a 7.5 yr-old male moose. Note the absence of hair follicles, numerous dermal ridges and collagen fibres orientated at right angles to fibres of adjacent undamaged tissue. Lillie's a-b, X 25.

Fig. 14. Longitudinal section of a scar at the terminal tip of the bell tail on a 14.5 yr-old male moose. Lillie's a-b, X 5.

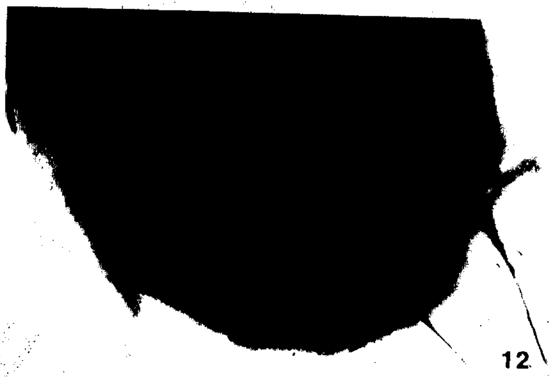
Fig. 15. Terminal tail portion of the bell from a 1.5 yr-old male moose killed in early December. The hair on the tail has been clipped. Note the large number of winter ticks, (*D. albipictus*), areas denuded of hair and yellowish debris sloughed from the skin surface (approximately actual size).

Fig. 16. Cross section of a winter tick (*D. albipictus*) attached to the epidermis of a bell tail from a 1.5 yr-old moose killed in late November. H and E, X 63. Note the presence of an amorphous, pink-staining material in the area of attachment.

Fig. 17. Longitudinal section of two tick (*D. albipictus*) larvae attached to the epidermis of the tail portion of a bell from a 2.5 yr-old cow. H and E, X 63. Note the accumulation of amorphous, pink-staining material present between the keratinized layer and the stratum granulosum of the epidermis beneath the feeding tick and numerous eosinophils among the pink collagen fibres of the underlying dermal papillary layer.

Fig. 18. A dense accumulation of eosinophils and some histiocytes beneath the keratinized layer on the bell of a female calf moose shot in November. Lillie's a-b, X 63.

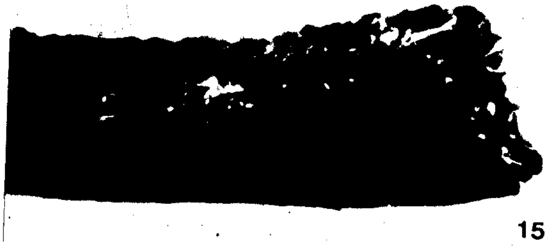
11



12

⑬

⑭



15

16

⑰

18

TABLE 12 The incidence of scars on the distal end of moose bells

	Males				Females			
			Length of bell tail (cm)*				Length of bell tail (cm)*	
Age (yrs)	N	No. with scars (%)	with scar	without scar	N	scars (%)	with scar	without scar
0.5	26	0 (0)	-	9.3 (15.5-12.9)	20	0 (0)	- -	8.1 (5.3-13.4)
1.5	58	0 (0)	-	13.7 (6.3-26.0)	50	0 (0)	- -	9.3 (4.5-14.3)
2.5	30	4 (13)	10.5 (0-18.5)	17.1 (5.9-25.5)	19	1 (5)	17.3 17.3	10.9 (5.8-17.5)
3.5	25	3 (12)	9.3 (0-21.2)	18.6 (6.2-35.5)	11	2 (18)	9.5 (8.4-10.5)	11.7 (6.9-16.1)
4.5	7	2 (29)	9.5 (3.2-15.7)	15.3 (8.1-20.2)	13	0 (0)	- -	11.5 (8.4-14.4)
(5.5-6.5)	20	8 (40)	13.3 (0-20.3)	15.6 (5.6-22.2)	15	0 (0)	- -	11.9 (8.5-15.5)
(7.5-8.5)	5	3 (60)	4.3 (0-12.8)	12.3 (9.0-15.0)	9	0 (0)	- -	11.3 (7.2-16.2)
9.5+	8	6 (75)	3.1 (0- 9.5)	13.7 (12.5-14.8)	19	1 (5)	0 0	11.4 (7.0-18.2)
Total	179	26 (14.5)			156	4 (2.6)		

* Mean length of bell tail and (range)

TABLE 13 The frequency and morphology of sack-type bells in moose examined

Age (yrs)	Sex	Frequency of sack-type bells in 1976 & 1977*	Bell length (cm) WH**	Bell length (cm) WOH***	Bell area (cm^2) WH	Bell area (cm^2) WOH	Scar size (mm)
2.5	♂	1/30	29.0	21.9	794	505	9 x 2
2.5	♂	*	24.0	16.0	526	328	12 x 5
3.5	♂	1/25	27.4	18.5	623	385	13 x 4
3.5	♂	*	27.3	16.5	772	432	14 x 5
3.5	♂	*	29.9	20.4	868	460	15 x 4
3.5	♂	*	31.0	22.5	830	476	10 x 4
5.0	♂	*	20.2	10.6	660	366	15 x 5
5.5	♂	1/9	34.0	24.0	1085	538	11 x14
7.5	♂	1/2	27.0	19.0	904	545	12 x 7
7.5	♂	*	30.8	22.0	1064	562	25 x 5
8.5	♂	1/2	30.0	24.7	963	587	12 x 2
10.5	♂	1/2	24.5	15.5	719	402	24 x 4
10.5	♂	*	24.4	17.5	801	535	12 x 4
10.5	♂	*	36.0	27.2	1083	654	21 x 4
11.5	♂	1/1	31.0	23.5	975	532	18 x 4
12.5	♀	1/1	26.5	18.0	678	389	8 x 3
12.5	♂	1/2	38.0	30.0	981	692	21 x 3
15.5	♂	*	26.0	17.5	743	459	15 x 4

* Incidental bells examined

** WH = With hair

*** WOH = Without hair

dermis. The keratinized layer over the scar was thickened. Dermal ridges were more numerous (Fig. 13) and there appeared to be a greater concentration of melanin granules in the stratum germinativum than in undamaged skin. Hair follicles were absent and the superficial dermis was often infiltrated with eosinophils (Fig. 14).

Bare patches or small, sparsely-haired areas were commonly seen in the mid-region of the tail of long bells. The density of winter hair on the bell tail of ten, 3.5-year-old males was examined. None of the bells had a scar on the distal tip. Hair densities were similar on the mid- and proximal regions of the 5 shortest bells and on the proximal and distal regions of the 5 longest (Table 14). Densities in the mid-regions of the combined sample were significantly lower ($P < 0.05$) than in either distal or proximal locations. The density of hair in the mid-region of the tail decreased slightly, but not significantly, with increasing tail length ($r = -.245$). Conversely, no changes in density were found in either the distal or proximal regions with increasing tail length. The ratio of guard (primary) hair to underfur (secondary) was similar in short and long bells in all three sample locations.

The moose winter tick, *Dermacentor albipictus*, was commonly seen on bells examined, particularly at the tip of the tail. The distribution of ticks on the tail portion of the bell and the host reaction to their feeding was investigated as a possible cause of changes noticed in bell morphology. The sample of bells examined (N = 54)

TABLE 14 Variation in hair density at three locations on the tail of moose bells*

			Location of hair sample		
	N	Tail length	Distal	Mid	Proximal
	5	15.8± 3.6 **	1236.2±163.4 **	810.4±198.2	873.6±192.3
		(13.5-18.0)	(1044-1560)	(596-1216)	(640-1296)
	5	24.2± 7.0	1059.2±169.2	807.6±161.1	1065.6±188.9
		(19.2-36.5)	(812-1416)	(576-1100)	(796-1436)
Total	10	20.0± 6.6	1147.8±185.7	809.0±175.8	969.6±210.1
		(13.5-36.5)	(812-1560)	(576-1216)	(716-1436)

* Bells of 3.5 year old males without scars
** Mean hair density/cm^2 ± S. D. (range)

came from 22 male moose killed October 11 - December 13 and 32 females killed October 7 - December 15. Ticks were present on the tail portion of all but 3 bells (Table 15, Fig. 15). These 3 animals were killed October 11 - October 20. Most ticks found throughout the hunting season were nymphs. However, a small proportion of larval or seed ticks were present on animals killed in October and November and a few seed ticks were found on a moose killed as late as December 3 (Appendix 4 and 5). A total of 6 adult ticks were present on the bells of 5 moose killed October 22 - December 6.

A mean of 0.6 ticks *per* cm^2 occurred on the tail portion of infected bells. The density of ticks was similar on males and females but calves had higher densities on both the proximal and distal portions of the bell than older animals ($P < 0.05$). The density of ticks was always greater on the distal portion of the bell than on the proximal portion ($P < 0.001$). The highest density found on the distal portion of the bell was 10.9 ticks *per* cm^2 on a male calf shot November 13. The number of ticks on the bells of one family group were remarkably similar. A female and twin female calves shot December 3, 1976 had 128, 133 and 121 ticks respectively (0.6, 2.1 and 2.0 *per* cm^2).

Some bell tails with large numbers of ticks were partially denuded of hair and considerable debris sloughed from the skin surface was usually apparent (Fig. 15). In sections of skin, an accumulation of amorphous pink-staining material was always present between the

TABLE 15 Density of D. albipictus nymphs on the proximal and distal tail portions of the bells of infected moose†

Age (yrs)	Sex	N	Proximal section		Distal section	
			Tick density*	Range	Tick density*	Range
0.5	♂	3	1.42±2.15	(0.17-3.91)	5.02±5.27	(0.79-10.92)
	♀	3	0.56±0.47	(0.03-0.92)	3.57±3.26	(0 - 6.38)
1.5	♂	7	0.37±0.32	(0.02-1.07)	1.60±1.92	(0.09- 5.76)
	♀	8	0.42±0.88	(0.02-2.59)	1.84±2.50	(0.08- 7.61)
2.5	♂	3	0.50±0.50	(0.18-1.07)	1.63±1.80	(0.39- 3.69)
	♀	3	0.10±0.16	(0.0 -0.28)	0.50±0.62	(0.05- 1.21)
3.5,4.5	♂	4	0.44±0.25	(0.31-0.72)	1.58±1.14	(0.43- 3.46)
5.5	♀	7	0.24±0.26	(0.01-0.62)	0.69±0.71	(0.04- 1.90)
6.5,7.5	♂	2	0.36±0.16	(0.24-0.47)	0.88±0.57	(0.48- 1.28)
8.5	♀	5	0.22±0.23	(0.06-0.63)	1.12±0.88	(0.49- 2.58)
9.5+	♂	2	0.01±0.00	(0.01-0.01)	0.06±0.02	(0.04- 0.07)
	♀	4	0.37±0.38	(0.07-0.93)	1.44±1.27	(0.41- 3.01)
Total	♂	21	0.52±0.83	(0.04-10.92)	1.90±2.53	(0.01- 3.91)
	♀	30	0.32±0.51	(0.0 -7.61)	1.44±1.85	(0.0 - 2.59)

* Mean/cm^2 ± S.D.

† Collection date of moose examined is shown in Appendix 4 and 5

keratinized layer and the stratium granulosum of the epidermis beneath attached ticks (Figs. 16 and 17). Eosinophils were numerous among the collagen fibres of the underlying dermal papillary layer. Small dense accumulations of eosinophils in a pink-staining matrix were commonly seen in skin sections immediately beneath the keratinized layer (Fig. 18). Ticks were seldom present adjacent to such lesions.

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. 19 and 20). A total of 28 heads (18 ♂♂, 10 ♀♀) 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 ♂♂, 5 ♀♀) and from the right in 13 (8 ♂♂, 5 ♀♀). 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 was filled with vinyl acetate by injecting it near the tip of the bell tail. Barium sulphate injected into the bell artery apparently was able to flow through the capillary bed and fill the venous system (Fig. 21 and 22). 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 lower 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

Fig. 19. 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; BA, bell artery; BV, bell vein. (Standard vascular system terminology after Sisson and Grossman. 1953.)


6
8
1
2
5
4
3
7
BA
BV

Fig. 20. 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, <u>bell vein</u>; 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, <u>bell artery</u>

(Standard vascular system terminology after Sisson and Grossmann. 1953.)

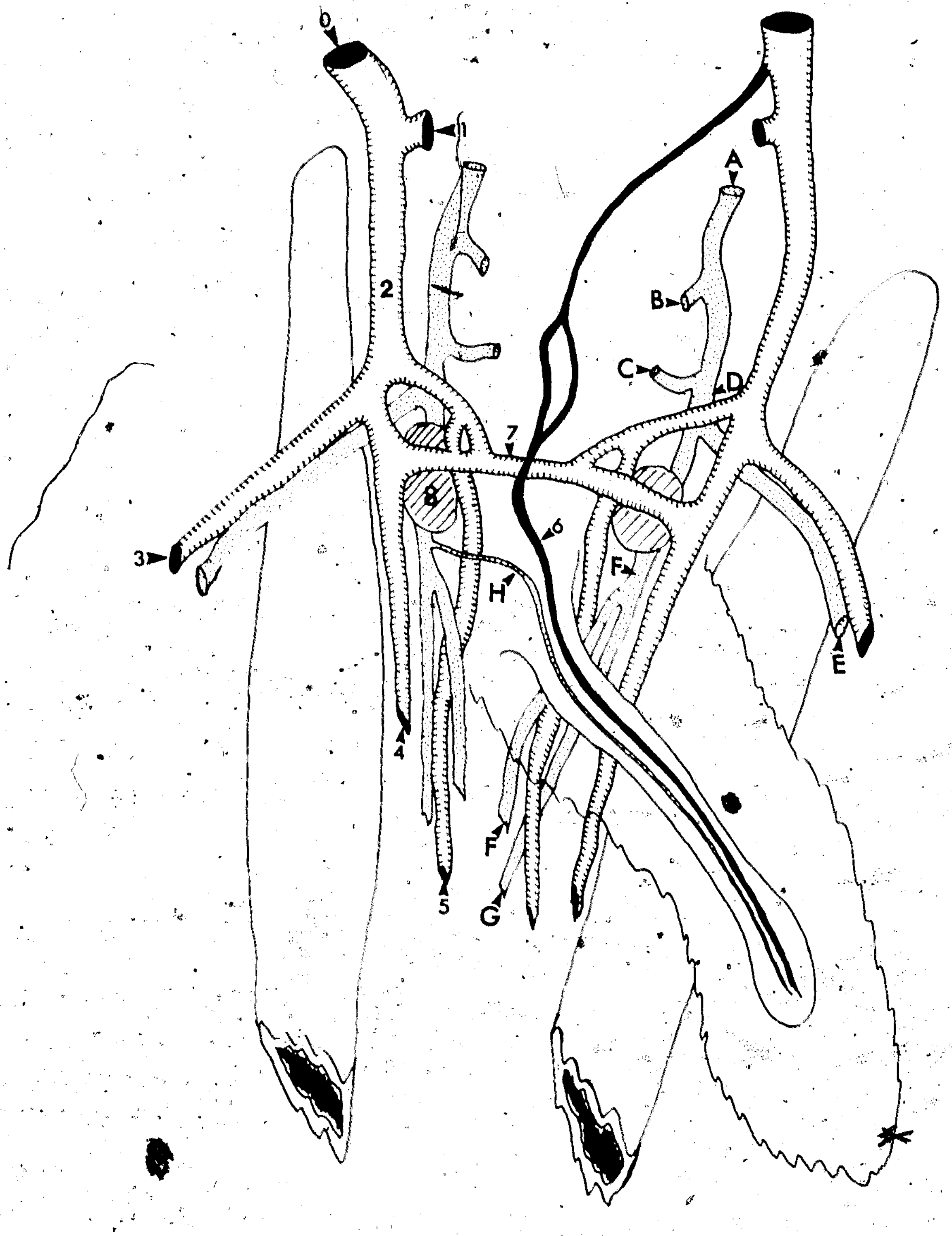

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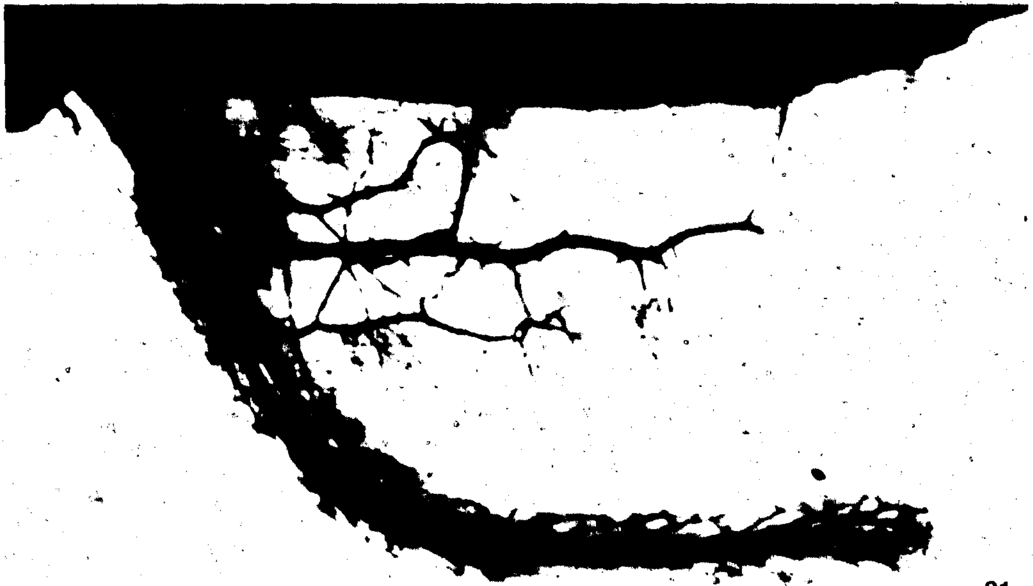
Fig. 21. Radiograph of the vascular system of a tail-type bell from a 3.5 yr-old male moose. Approximately 1/2 original scale. (◄ indicates bell artery).

Fig. 22. Radiograph of the vascular system of a sack-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).



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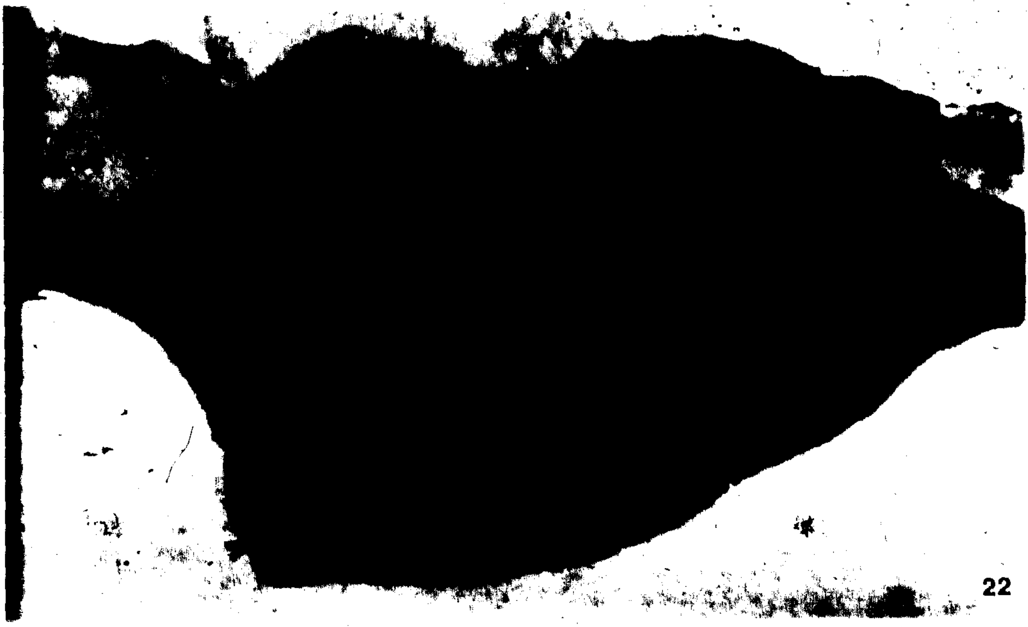

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region. A male calf submitted whole provided the single opportunity to follow the bell vein to its junction with the jugular vein. In this animal, the bell artery arose from the right lingual and the bell vein joined the left jugular. In sack-type bells without a tail, the major arterial and venous circulation was similar to that found in the dewlap of bells with a tail (Fig. 22). There was usually a prominent network of small vessels in the region adjacent to the scar on sack-type bells but the branches of the bell artery and vein that serve the tail of typically shaped bells were not apparent.

The extent of arterial branching in the tails of 2 bells is illustrated by vinyl acetate casts (Figs. 23 and 24).

The bell of a developing fetus was visible as a small bud on the ventral surface of the neck as early as late November (Fig. 25). By mid-term (February-March), the bell was still without hair and was 2-4 mm long. The bell of mid-term male fetuses was always longer than that of females. There was often considerable difference in the length of bells on twins of the same sex.

At birth bells were fully haired and mean lengths were 35.5 ± 9.6 mm (WH), 25.6 ± 9.0 mm (WOH) and 13.3 ± 5.8 mm tail (WOH) on 8 males and 25.9 ± 5.8 mm (WH), 18.7 ± 5.1 mm (WOH) and 9.8 ± 3.3 mm tail (WOH) on 9 females. The jaw lengths of full term male and female fetuses were similar (21.0 ± 2.4 cm).

The bell of moose $\geq$ 0.5 yr is typically comprised of a loose hanging non-turgid sack-like dewlap and a narrower pendant tail. The

Fig. 23. A vinyl acetate cast of the arteries in the bell tail and a portion of the dewlap from a 3.5 yr-old male moose. Approximately 2/3 original scale. Original bell length; WH = 45.6 cm., WOH = 38.8 cm., tail = 19 cm.; bell profile area; WH = 953 cm^2, WOH = 457 cm^2, dewlap = 401 cm^2, tail = 60.0 cm^2.

Fig. 24. A vinyl acetate cast of the arteries in the bell tail from a 2.5 yr-old male moose. Approximately 2/3 original scale. Original bell length; WH = 58.0 cm., WOH = 51.0 cm., tail = 30.0 cm.; bell profile area; WH = 1123 cm^2, WOH = 601 cm^2, dewlap = 535 cm^2, tail = 72 cm^2.

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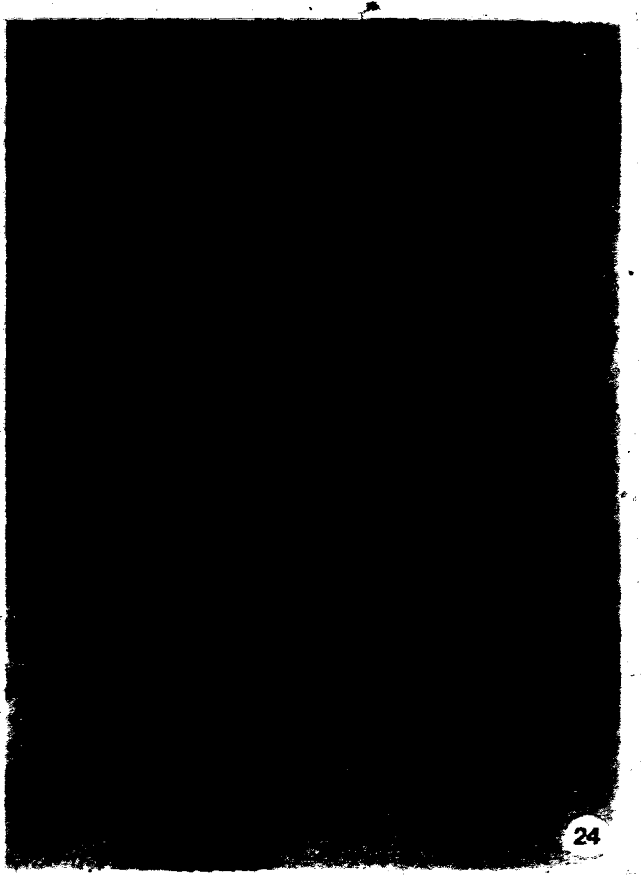

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Fig. 25. The bell of a developing female moose fetus visible as a small bud on the ventral surface of the neck in late November. Approximately 1/2 actual size.

Fig. 26. Lateral view of a bell from a 14.0 yr-old cow moose killed in early June. Approximately 2/3 actual size. Note the new growth of summer hair and darkly pigmented skin.

Fig. 27. A fall-killed, female calf moose with a dense insulating coat of winter hair (partially clipped) covering the entire bell. Approximately 1/4 actual size.

Fig. 28. Saggital section of a mid-term (Feb. 17) female fetal bell. Lillie's a-b, X 25. Note the developing hair follicles and the extensive pink staining capillary network.

Fig. 29. Saggital section of a March 7th female fetal bell. Lillie's a-b, X 25. Note the developing bell vein running dorso-ventrally within the central dermal core of collagen fibres and the deeply embedded hair follicles with hair shafts beginning to emerge and protrude through the epidermis.

Fig. 30. A cross section of the tail portion of a near term (May 8th) female fetal bell. Lillie's a-b, X 25. Note: portions of the bell artery (left centre) and vein (right centre) are embedded within the central collagen core and surrounded by a layer of hair follicles (deep blue).

Fig. 31. A cross section of the tail portion of a term (May 21) male fetal bell. Lillies a-b, X 6. Thick bundles of well organized pink-staining collagen surround arteries and veins within a common central reticular layer of the dermis. A thin outer epidermis encapsulates blue-staining developing hair follicles embedded in dermal tissue.

Fig. 32. Saggital section of a near term (May 4th) female bell showing features similar to those in Fig. 31. Lillie's a-b, X 4.


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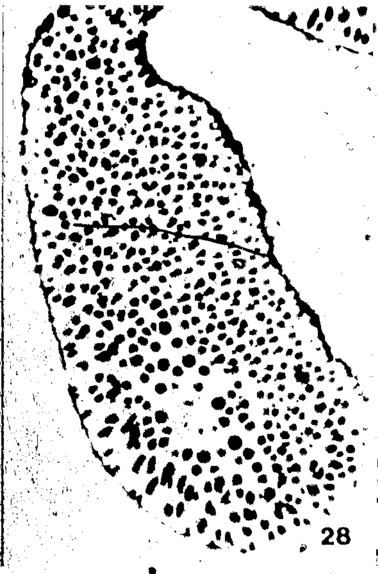
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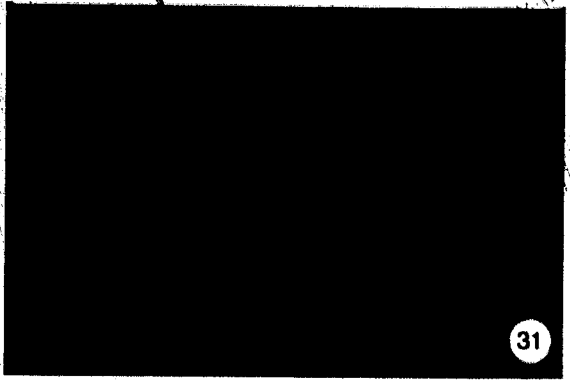
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spatula-shaped tail is most easily observed from late May to the end of July after the winter hair has been shed (Fig. 26). By early fall the entire bell is covered with a dense insulating coat of winter hair and the tail becomes less conspicuous (Fig. 27). The tail on bells clipped of hair, narrows mid-way along its length and is frequently bulb-like at the distal end. The narrow isthmus on all tails measured in side view was 22.2 ± 4.7 mm wide and 10 ± 2 mm thick. The distal bulb widened to 30.8 ± 4.7 mm.

The histological description of the bell is based on the examination of approximately 500 sections from 28 males and 12 females representing all age groups. The bell of mid-term fetuses was covered with an epidermis 5 - 10 cells thick. Primary and secondary hair follicles surrounded by dense capillary networks were visible and some contained a short hair shaft extending into the overlying epidermis (Fig. 28). Developing follicles were formed as a plug of epidermal cells which grow down into the dermis. Later in the fetal period, the hair shaft begins to emerge from the follicle (Fig. 29) and protrude through the epidermis which at this time is much thinner (20 μm). Sebaceous glands associated with both primary and secondary follicles are readily identified at this stage. A single branching artery and a vein enters the bell and runs dorsoventrally within the central dermal core of collagen fibres (Figs. 29 and 30).

At birth thick bundles of well organized collagen surround arterial and venous vessels within the common central reticular layer of the dermis (Fig. 31). Primary hair follicles were more deeply embedded in dermal collagen (1.0 - 1.5 mm) than secondaries (Fig. 32). The entire bell is covered with fine hair 50 - 200 µm in diameter and 13.4 ± 6.9 mm in length. The epidermis begins to thicken slightly with the appearance of an outer keratinized layer. Arrector pili muscles and sebaceous glands were observed in association with maturing follicles. Sweat glands were not identified in 8 fetal bells examined.

The outer epidermal surface on bells of growing moose $\geq$ 0.5 yr is typically a thin (15 - 40 µm) layer of squamous epithelium 2 - 5 nucleated cells thick, overlain by a superficial layer of keratin. The epidermis thickens somewhat and is darkly pigmented during the annual spring hair replacement period. Melanin granules occuring in the basal layers of the epidermis and developing hair are chiefly responsible for the dark appearance of skin and newly growing summer hair (Fig. 26). As the season progresses, growing hair and underlying epidermis take on a pale almost white appearance due to reduced melanin production (Fig. 27).

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, arrector 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 collagenous 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 providing nutrition to the overlying epidermis.

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 µm) coarse guard hairs and shorter finer diameter (20 - 50 µm) hairs (Figs. 33 and 34). Each hair follicle is surrounded by two or three sebaceous holocrine glands and bundles of arrector pili muscles. Sebaceous secretion tested positive with APT stain and negative with PAS, indicating the presence of anionic heteroglycans (acid muco polysaccharides). During fall and winter, sebaceous glands were generally lobate in shape and proportional in size to their associated hair follicle. They appeared larger in summer than in winter in both sexes. Smooth arrector muscles (Fig. 35) originate in the dermal papillary layer and insert into the connective tissue sheath of each hair follicle. Both sebaceous glands and arrector muscles appeared somewhat larger and more irregular in males than in females.

Sweat glands with their tightly coiled basal secretory tubule lie deep in the dermal reticular layer between hair follicles (Fig. 34). Although all sweat glands were closely associated with

Fig. 33. Cross section of bell skin from a 9 month-old male moose. Two large primary hair shafts (solid yellow) are surrounded by purple staining sebaceous glands. Two smaller secondary hair shafts appear left of centre in dark blue staining dermal collagen. The outer epidermal surface (15-40 µm, dark purple) is overlain by a superficial layer of deep red staining keratin (lower left). Four developing hair follicles (bright red and yellow brush-ends) of two distinct sizes are sectioned tangentially. Small (20-50 µm) sweat gland ducts are scattered between hair shafts and follicles. Martius yellow-crystal scarlet aniline blue (MSB), X 63.

Fig. 34. Longitudinal section of bell skin adjacent to a terminal scar from a 9.5 yr-old male moose. One large hair follicle (dark blue) is to the left of two blue staining sweat glands with their tightly coiled basal secretory tubules embedded in the pink-staining dermal reticular layer. Lillie's a-b, X 25.

Fig. 35. Longitudinal section of bell skin from a 9 month-old male moose. An arrector pili smooth muscle (dark blue) runs diagonally from lower right to upper left in dermal collagen. Portions of a sweat gland secretory tubule and duct are stained light purple in cross section. A sebaceous gland (light purple) appears in the lower left. MSB, X 160.

Fig. 36. Section of a sweat gland secretory tubule from bell skin of a 9 month-old male moose. Secretory cells are surrounded by a basal lamina staining deep blue. A few myoepithelial cells can be seen partially winding around the tubule. MSB, X 400.


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hair follicles it was not possible to determine if their ducts (15 - 25 µm lumen diam.) connected to a follicle or emptied directly to the epidermal surface (Fig. 35). The larger coiled secretory tubule of the gland (25 X 120 µm lumen diam.) is lined with a simple low columnar or cuboidal epithelium supported by a distinct basal lamina staining deep blue with MSB (Fig. 36). The spherical nucleus occupies a basal position within the cell and contains 3 - 4 prominant nucleoli staining dark blue with Lillie's and pink with MSB. The cell cytoplasm appears as a fine purple-staining net with unstained areas between strands. A few myoepithelial cells were seen partially winding around the tubule between the base of the cells and the basal lamina. The nucleus of these spindle-shaped cells is elongated and their cytoplasm stained reddish with MSB. The secretory tubule narrows into a smaller diameter excretory duct which is lined with a double layer of darkly staining cuboidal cells. Cells forming the inner layer of the duct stain more intensely along the surface bordering the lumen. The duct is surrounded by a basal lamina and myoepithelial cells appear absent. The staining properties of the gland cells and their size, shape and dermal depth were similar in specimens of different ages and sex. The highest concentrations of sweat glands observed in bell tissue was in the distal tail area on either side of scar tissue. However, they may have been just more conspicuous adjacent to scar tissue because saggital rather than transverse sections were examined and hair follicles were less numerous.

Sweat glands found in tarsal tissue were larger, more numerous and well defined than sweat glands seen in skin of the bell or cheek. The basal secretory portion of the sweat gland was more deeply embedded in dermal tissue than glands examined elsewhere. The lining epithelial cells were cuboidal with a basal nucleus and nucleoli staining almost black with MSB. Apical portions of the epithelial cells were sometimes seen free in the lumen of the tubule in tarsal as well as bell tissue.

The cytoplasmic network of interconnected strands in tarsal sweat glands stained purple and contained pink-orange inclusion bodies. Myoepithelial cells were numerous beneath the cuboidal epithelium and stained deep orange with MSB. The depth of hair follicles and length of arrector pili muscle in tarsal gland tissue were twice those found in either cheek or bell skin. Cheek sweat glands appeared smaller, less numerous and more poorly defined than sweat glands in either bell or tarsal gland tissue.

DISCUSSION

In northwestern Ontario, the bell on male moose is usually longer and has a greater profile area than that on females. The longest bells were found on males 2.5-3.5 yr old. In older males, a sack-type bell without a tail was common. A scar was present at the distal end of all sack-type bells suggesting a tail had once been present but was lost.

Similar observations have been made on moose elsewhere. On Sibley Peninsula, east of Thunder Bay, Ontario, moose were photographed while frequenting salt licks during spring and summer (P. Frazer, Ont. Min. Nat. Res., Maple, Ont., pers. comm. 1979). Sack type bells or bells with a very short tail (<3 cm) were seen on 13 of 21 mal[illegible]ose estimated to be 3 yr or older. Younger males (N=24) and all females (N=44) had a bell with a conspicuous tail portion. In Newfoundland, the bells of moose killed by vehicles were measured (E. Mercer, Newfoundland Department of Tourism, St. John's, Newfoundland, pers. comm. 1978). The bell on males (N=92) was consistently longer than that on females (N=35) and the longest bells occurred on males 3-4 yr old. A small sample of bells from *A. a. gigas* collected near Soldotna, Alaska were sent to the author by A. Franzmann, Alaska Department of Fish and Game, Soldotna, Alaska. The bells of 7 females (0.5-14 yr) and 2 males (2 yr) were similar in shape and size to those on moose in northwestern Ontario and all had a tail portion. However, sack-type bells are commonly seen on older bulls in Alaska and a tissue scar can be seen on the distal edge of such bells (A. Franzmann, pers. comm. 1979).

Sokolov (1964) mentioned that the longest bells on *A. a. alces* in central Soviet Union occur on males 3-4 yr and the bell is shorter and broader on older males. Although most workers agree that old male moose generally have short broad bells, long bells are occasionally seen. The tail portion of a bell from a 11.5 yr old male killed near Geraldton, Ontario measured 29.0 cm (C. Greenwood, Ont. Min. Nat. Res. Geraldton, Ont., pers. comm. 1978).

The length and morphology of the bell may vary on moose in different parts of their range. Dr. C. H. D. Clarke (retired, chief Fish and Wildlife Branch, Ont. Min. Nat. Res. Toronto, Ont., pers. comm. 1977) mentioned that moose in the Rocky Mountain Parks of Western Canada generally had longer bells than he had seen on moose elsewhere in Canada. Some moose in the Interlake Region of central Manitoba have exceptionally long bells (some exceeding 76 cm) and were believed by Crichton (Manitoba Department Mines, Resources and Environmental Management, Winnipeg, Manitoba, pers. comm. 1978) to be 15-20 cm longer than bells seen on moose in other parts of Manitoba. The longest bell reported in the literature (96 cm excluding hair) was from a female shot in eastern Manitoba in 1903 (Seton 1929). It is interesting to note that long, tail-like bells are rarely seen on moose (*A. a. alces*) in eastern Europe. Bells on moose in Norway were described by Lykke (7660 Vuku, Norway, pers. comm. to A. Bubenik, 1978) as pad-like and not usually conspicuous on females. Moose in Sweden are also reported to have short inconspicuous bells (Lönnberg 1923).

Sack-type bells seen commonly on older males in the present study were without a pendulous tail. There is some evidence that the tail portion may be lost as a result of freezing. During January and February of 1953, the Ontario Department of Lands and Forests collected a number of moose on Big Island in Lake of the Woods, northwestern Ontario. The tip of the bell was described as "frozen stiff" on several moose examined immediately after being shot (R. Hepburn, Ont. Min. Nat. Res. Maple, Ont., pers. comm. 1979). In mid winter, 1978, a Manitoba Provicial Park employee found what appeared to be the terminal tail portion of a moose bell which was about 15 cm long in an open area on a moose trail. There was no blood at the site or anything on which the bell might have caught and been torn off (V. Crichton, pers. comm. 1978). Dr. A. Bubenik, (pers. comm. 1977) has spoken to trappers in Alberta who claim to have found pieces of frozen moose bells during winter. In the Soviet Union, Knorre (1959), Sokolov (1964) and Kozhukhov (1965) reported that the bell of moose may freeze and fall off during the first or second year of life and leave either a shortened tail or a broad fold of skin, depending on the original length of the bell.

The likelihood of the bell tail being lost by freezing or other causes may be related to its length. In the present study, the tail portion of the bell 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. Histological examination and latex injections gave the impression that the narrow isthmus of the bell tail was less vascularized than either the proximal or distal regions. 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. Suitable skin temperature may not be maintained as the bell tail increases in length making long tails more susceptible to freezing in cold weather.

It is difficult to assess the possible role of ticks in causing the loss of the bell tail. The densities of ticks on the distal end of the bell was 4 to 5 times that reported anywhere on moose by Addison *et al.* (1979) and Samuel and Barker (1979). The high concentrations at the distal end of the bell may reflect a positive geotropic response by the ticks. Other explanations, however, are equally tenable. Ticks may more readily attach on to moose at the dangling bell tip. They may be attracted to the well vascularized bulbous end of the bell or may simply be more difficult to dislodge from this site. Ritchey and Edwards (1958) reported moose in British Columbia thrashing their heads in willow bushes and scratching their head and ears presumably in attempt to rid themselves of ticks in late winter. Dense accumulations of ticks did cause skin irritation and apparently hair loss from the tail of some moose bells examined in northwestern Ontario. Ticks were believed responsible for the loss of hair from extensive regions of the body of moose (Addison *et al.* 1979; Samuel and Barker 1979) sometimes causing death due to excessive heat loss in late winter (Samuel and Barker 1979). The large numbers of ticks feeding on the bell may predispose it to freezing but it should be noted that winter tick is not known to occur in Alaska (Wilkinson 1967) where older moose commonly have a sack-type bell without a tail (A. Franzmann, pers. comm. 1979).

One objective of the present study was to discuss how the variability in shape and size of the bell might influence social interactions between moose. It is presumed that many mammals communicate visual messages by directing their attention to the anal and head poles of conspecifics and interpret specific expressive characteristics and movements (Portmann 1952, 1961; Young 1957; Bubenik 1973). Species specific contrasting colour patterns adorn the rumps of North American pronghorn, many old-world antelope, mountain sheep (*Ovis* spp.), deer (*Odocoileus* spp.) and wapiti, *Cervus canadensis* Erxleben (see Guthrie 1971). Elements of the head which may transmit information include antlers, horns, eyes, ears, lips, pelage colour and specific hair patterns or structures. Visual sex-dimorphic features of the head such as different colouration size or presence and absence of antlers and horns have been identified in many ungulates including red deer, *Cervus elaphus* L.; chamois, *Rupicapra rupicapra* Frisch; ibex; white-tailed deer and some antelope (Bubenik 1966, 1975; Walther 1974; Smith 1977; Meile and Bubenik 1977).

In moose, the anal pole, with the exception of the light contrasting female vulval patch (Mitchell 1970; Lent 1974) presumably projects little visual releasing stimulus. Visual releasers in this context are sign stimuli capable of triggering or releasing a responding behaviour (Lorenz 1935). Distinctive features on the head include variation in antler shape and size among males, and pelage colour and bell morphology in both sexes (Altmann 1959; Mitchell 1970; Eibl Eibesfeldt 1970; Bubenik 1973, 1975; Bubenik *et al.* 1977, 1978, present study).

Bubenik *et al.* 1977 have generally defined four social classes of moose (calves, teens, primes and seniors) on the basis of antler size in males and facial pigmentation in both sexes. The morphology of the bell is also somewhat distinctive in animals of each of these social classes. In calves the bell is short and has a narrow nondescript tail. Teen males (1.5-3.5 yr) have a bell with a long tail and little dewlap. Prime males (4.5-8.5 yr) have a medium to short tail attached to a broad dewlap. Senior males have a broad sack-like dewlap, very often without a tail. Teen, prime and senior females on the other hand, usually have a bell with short to medium length tail and little dewlap which is similar in appearance to the bell of 1.5 year-old males.

Antlers and horns can be potent visual releasers that serve an important function in establishing a ranking order as well as being sexual attractants (Geist 1966; Eibl Eibesfeldt 1970; Bubenik 1973). Bubenik (1975) using an artificial caribou (*Rangifer* spp.) head concluded that antlers overshadow all other releasers including human scent. Moose are able to estimate rank of their own antlers and respond accordingly to antlers of lower, higher or the same rank at considerable distance (Bubenik 1973). High ranking alpha male red deer apparently drop in rank after antler loss (Hediger 1954; Bubenik 1968) but reacquire their former rank after the beta male also looses his antlers (Portmann 1961). Bell shape and size may partially compensate for antler loss in maintaining a ranking order during the unantlered period. The bell may also function as a short distance releaser among mixed sex and age aggregations commonly observed in the post-rut, early winter period (Bubenik, pers. comm. 1979).

Visual messages are conveyed to conspecifics in a variety of body postures and movements of the head, neck, and body (Smith 1977). The *present threat* where an animal aligns itself broadside to an opponent is widely employed by bovids (Schloeth 1956, 1958; Walther 1958, 1961; Tembrock 1968). Among cervids such visual self-exposure has been described in *Odocoileus* by Cowan and Geist (1961) and is used by caribou (Bergerud 1974) and moose (Altmann 1959; Geist 1963; Lent 1974) during the rut. Linked with the broadside position is the presentation by some species including mountain goats (Geist 1965) and Nilgai bulls (Walther 1977) of additional structures such as beards and manes which can be erected. The lateral posture makes the animal appear as long and broad as possible (Walther 1977). The apparent size of bovids is believed an important component in establishing rank between individuals

(McPhee *et al.* 1964; Smith 1977). Moose present their full body outline to an opponent when standing broadside. It is in this position that the bell may best be viewed by conspecifics. Erector muscles and possibly increased blood flow facilitates the raising of guard hairs in certain zones thus enlarging the overall profile. Both Skunke (1949) and Knorre (1959) have described the swelling of the bulls neck during rut. The author has personally observed the ability of moose to change bell outline by erecting the hairs along the jaw near the base of the bell. Lateral self-exposure allows opponents to 'size' each other up visually and gain reciprocal information on antler and bell size and body condition (Lent 1974). The majority of male-male encounters end with one opponent withdrawing and avoiding any physical contact (Murie 1934; Peterson 1955; Markgren 1969).

A variety of possible expressive neck postures including neck downward, upward, forward and to the side may occur during the broadside display (Walther 1974). The elevation of the head and neck increases the animals apparent size and is considered an essential component in threat displays among a variety of ungulates (Walther 1977). The possibility exists that some species with relatively short necks compensate by presenting additional structures such as the bell or beards and manes which may be erected. The beard of the mountain goat and bison both increase the overall body profile (Lott 1974; Geist 1965). The head high threat or extended head posture in moose is interpreted by Geist (1963) as an aggressive intimidation display used by dominant animals. Murie (1934) often observed cows at salt licks facing each other with muzzles held high and ears lowered. Geist (1963) described the head high threat when males were in velvet and, along with Kozhukhov (1965), the head low threat with hair raised on withers and rump after antlers had been dropped. Bubenik (1973) also observed the head of prime males bent downward or lowered so it nearly touched the ground during frontal interactions with his artificial moose head. Such postures may display a change in visual head colour pattern, the architecture and size of antlers and perhaps the shape and outline of the bell.

Sexual dimorphism of the bell on moose ≥ 1.5 yr has been demonstrated. Such variation may play an important social role among early winter post-rut aggregations when snow cover could increase visual contrast. Small cervicorn antlers among young males (1.5-2.5 yr) must be viewed at relatively short distances and frontally to estimate rank or individuality (Bubenik 1973). Long tail bells commonly found on such animals could help re-enforce their lower social rank when viewed from the side. Antlers of bulls ≥ 3.5 yr have in the view of Bubenik *et al.* (1977, 1978) primarily offensive characteristics. The protective elements of converging points and wide palms develop between the 4th and 7th antler cycle. Co-incidentally this is also the age at which males tend to lose their long tail bells and develop a broader more sack-like structure.

Crombrugghe and Vorreyer (1968) have identified a progressive deepening of the red deer neck and dewlap with increasing age. During courtship the estrus female may give preference in mate choice to visual indicators of age and experience (Smith 1977). A prime bull with large antlers and a broad deep sack-type bell not only demonstrates a prime social rank but an animal that has gained experience in extracting critical nutrients from the environment (Chapman 1975; Taber 1958; Bubenik 1959, 1966). In mountain goats where both sexes have a similar chin beard it is believed by Geist (1965) that the presence of the beard on males may diminish the agonistic tendancy of the female during the breeding season and reduce the chances of the male being attacked and wounded.

If the bell is indeed utilized as an optical cue one must consider several additional factors. The simplest visual releasers are found in animals inhabiting dense cover while the most complex are found in species adapted to life in open country (Bubenik 1975). Studies of moose visual interactions have been largely limited to open tundra-type habitats such as Wyoming (Altmann 1959; Houston 1968, 1974), British Columbia (Geist 1963) and Alaska (Bubenik 1973; Lent 1974). However, over much of its range the moose is essentially a non-gregarious, sylvan species, (Murie 1934, de Vos *et al.* 1967; Geist 1971; Houston 1974). Such habits may reduce the need for a variety of well developed body signalling cues. Conspicuous visual signals might tend to unduly advertise the animals presence especially toward predators (Mailer 1968;

Eibl - Eibesfeldt 1970; Hailman 1977). A great deal of boreal moose activity takes place at night, dawn or dusk and generally in wooded habitat where light becomes diffused. With the exception of the light colouration of the inner ear (Seton 1929) and the light chin patch in female calves (Bubenik *et al.* 1977), the homogeneous dark, brown-black pelage produces a minimum amount of reflection or visual contrast which might aid in attracting conspecifics, particularly during the snowless period. The bell likewise possesses no specific contrasting colour patterns and tends to blend cryptically into the overall dark body colouration.

The bell is however a distinctive structure that is particularly conspicuous on some individuals but any suggested role of the bell in visual communication is pure supposition and will be extremely difficult to quantify. Perhaps the most fruitfull approach for further research might be the use of an artificial dummy head with interchangeable bell-profiles similar to that described by Bubenik (1973) for testing behavioral responses to a variety of moose antler sizes and shapes.

A final objective of the present study was to investigate the bell and its associated skin glands as a possible source of pheromone-like secretions. Some reports in the literature suggest this as a function of the bell. Zschetzche (1959) maintained that during the rut, the hairs of the lower part of the bell tail of Swedish moose (*A. a. alces*) were covered by an odorous secretion which originated from a wide opening at the terminal end of the bell into which a knitting needle could be inserted. Observations on North American moose indicate that considerable attention is directed toward the head by courting pairs during the rut period. Occasionally a bull will rest or rub his chin, neck and bell on some part of the female (Thompson 1949; Dodds 1958; Lent 1974). This behavior could be derived from the neck fight seen in other ungulates (Geist 1971; Walther 1973) but could also function in some way to transfer scent between individuals (Lent 1974). Female moose in estrus have been observed smelling the anal-genital area of the male and then prodding or pushing the muzzle against his flank and neck (Geist 1963; Lent 1974).

In this study, an opening was never seen at the distal end of the bell nor were distinctive odours or suspected secretions ever detected on the bells examined. Seton (1929) who examined "many" bells also failed to find discernable scent glands, exudate or particular odour on moose bells. The terminal opening in the bell reported by Zschetzche (1959) could have been an exposed blood vessel, scar or skin fold at the tip of an injured or previously frozen bell. Sebaceous and sweat glands, however, were present in the skin of the bell. The most detailed descriptions of these glands and understanding of the nature of their secretions result principally from studies of human skin but also from studies of other mammals.

Sebaceous glands are located in the dermis and connect by a short duct to the side of an adjacent hair follicle. Each gland is usually comprised of several alveoli or acini encapsulated by a layer of connective tissue (Leeson and Leeson 1976). The alveoli are filled with stratified epithelial cells. The germinative cells around the periphery of the alveolus stain densely basophilic. These cells become more cuboidal and filled with fat-like droplets as they are pushed toward the neck of the alveolus. Here the cells rupture and release their contents termed sebum, which in humans, has been identified as a mixture of cholesterol, phospholipids and triglycerides (Strauss and Matoltsy 1973). The discharge of sebum is aided by contraction of the arrector pili muscle and pressure of increasing gland content (Leeson and Leeson 1976). It is generally acknowledged that sebum serves to oil the hair and prevent drying of the skin (Ryder 1973) but it may also be involved in olfactory or pheromonal communication (Quay 1977).

The sweat glands of mammalian skin are classified as either eccrine or apocrine. These have traditionally been thought of as two distinctly different specialized forms of sweat glands but some recent authors (Ryder 1973) suggest the differences between eccrine and apocrine glands may not be as great as once thought. Both type are tubular in structure and are unbranched. Eccrine sweat glands are widely distributed in human skin but are largely restricted to unhaired areas of skin in other mammals (Strauss and Matlotsy 1973).

The coiled secretory portion of the tubule is lined by a simple layer of columnar or cuboidal epithelial cells, some of which stain basophilic and others which are eosinophilic. The lumen of the tubule is relatively narrow. An incomplete layer of myoepithelial cells surrounds the secretory portion of the tubule. The duct of the eccrine gland is not connected to hair follicles but empties directly to the skin surface *via* a corkscrew-like duct. In humans the sweat secreted by eccrine glands is a transparent, watery liquid containing a variety of ions including sodium, chloride and potassium as well as some urea and lactate. Sweat functions primarily in facilitating evaporative heat loss.

Apocrine sweat glands are found over the entire skin surface of most mammals. They have a larger tubule lumen, are less coiled and more deeply embedded in the dermis than are eccrine glands (Leeson and Leeson 1976). The secretory portion of the tubule is lined with simple cuboidal or columnar cells with a rounded basal nucleus containing a prominent nucleolus. These secretory cells are eosinophilic (Strauss and Matoltsy 1973). Numerous spindle-shaped myoepithelial cells surround the secretory portion of the tubule and are thought to aid in emptying the contents of the gland *via* a fairly straight duct connected to a hair follicle. In contrast to eccrine sweat glands, apocrine gland secretions contain protein which in many mammals is suspected of being important in olfactory communication (Schaffer 1940; Quay 1968, 1977; Strauss and Ebling 1970; Quay and Müller-Schwarze 1970).

Concentrations of skin glands in particular regions of the body are well known among the Cervidae (Schaffer 1940; Quay 1955, 1959; Taylor 1956; Graf 1956; Müller-Schwarze 1967, 1971; Quay and Müller-Schwarze 1970, 1971; Müller-Schwarze and Müller-Schwarze 1971; Bubenik *et al.* 1979). These include the so-called tarsal, metatarsal, interdigital, caudal and antorbital glands. In those ungulates with prominent tarsal glands such as *Odocoileus* spp., *Rangifer* spp. and moose, animals commonly rub the hocks together as urine is directed over the glands. Müller-Schwarze *et al.* (1977) reported that black-tailed deer commonly sniff the mixture of tarsal gland secretion and urine produced in this way. Moose have conspicuous tarsal glands on the inside of the hock joints, interdigital glands between the toes and antorbital glands (Sokolov, 1964; Bubenik *et al.* 1979). Specific glandular areas in the metatarsal region may be present among some moose in Europe (Schaffer, 1940) but are not readily visible on moose in northwestern Ontario and have never been investigated specifically.

The localized glandular areas have been studied histologically in some cervids (Quay 1955, 1959; Polukhov and Kulikova 1958; Sokolov 1964; Quay and Müller Schwarze 1970, 1971; Müller-Schwarze and Müller-Schwarze 1971) and to some extent their secretory products have been characterized by histochemical techniques (Brownlee *et al.* 1969; Bubenik *et al.* 1979) but little is known of the precise role such products may play in olfactory communication between animals. In such areas, apocrine sweat glands are numerous and sebaceous glands and arrector muscles are larger than found in surrounding skin tissue (Quay and Müller-Schwarze 1970, 1971). Specialized hairs termed 'osmetrichia' were reported by Müller-Schwarze *et al.* (1977) in the tarsal gland of black-tailed deer and are believed to aid in specialized scent retention and distribution. The cursory histological examination of tarsal gland tissue in the present study revealed the presence of apocrine-like sweat glands similar in appearance to those reported in tarsal gland tissue of other cervids (Quay 1955, 1959; Quay and Müller-Schwarze 1970, 1971).

In the skin of the bell, sebaceous glands were present in the mid-term fetus as well as in older animals where they appeared larger in males than in females. Sebaceous glands in the bell also appeared to be larger in summer than in winter. Similar seasonal differences in the size of sebaceous glands in body skin have also been reported in moose by Sokolov (1964) and in roedeer, *Capreolus capreolus* L., by Schumacher (1936) and in pronghorn by Moy (1969, 1970). It is unknown whether sebaceous gland secretions include any specific pheromone or chemical scent cues (Quay and Müller-Schwarze 1970).

Sweat glands observed in the skin of the bell had a smaller lumen diameter, were less numerous, more tightly coiled and not as deeply embedded in the dermis as apocrine-like glands seen in tarsal glands. Although these sweat glands were closely associated with hair follicles it was not possible to determine whether their ducts emptied into the follicle or directly onto the epidermal surface. Their morphology and staining properties most closely resembled glands classified as eccrine in human skin by Strauss and Ebling (1970); Bloom and Fawcett (1975) and Leeson and Leeson (1976). They were similar in appearance to sweat glands seen in skin of the cheek. Sokolov (1964) also found the histology and distribution of sweat and sebaceous glands in the bell similar to those in body skin. It therefore appears doubtful that the sebaceous and sweat glands in the moose bell are any more specialized than those elsewhere in general body skin.

Although it appears unlikely that the bell is a specialized secretory area, it could possibly serve indirectly to disseminate scent. The male grey waterbuck, *Onotragus megaceros* Gray and *Capra* spp. for example, splash urine and sometimes sperm into the hair or beard of the throat region (Lott 1974; Walthers 1977). This behavior has not been observed in moose but males dig pits in the earth during the breeding season into which they urinate (Kakies 1936; Skuncke 1949; Thompson 1949; Altmann 1959; Geist 1963; Lent 1974). The bulls may mark their antlers with urine-soaked earth before laying down and rolling in the rut pit (Van Wormer 1972). Moose in Norway have a strong odour associated with the head region which may result from contact with rut pits or be produced by skin glands (Lykke per. comm. to A. Bubenik 1978). Self-marking with urine has been described in bison and reindeer (*Rangifer* spp.) by Lott (1974) and Espmark (1964) respectively. These authors have suggested that the odour of individual male urine may permit bulls to use pre-established dominance relations effectively in the dark. One might speculate that the dangling moose bell, if marked with urine might similarly serve to communicate information to conspecifics.

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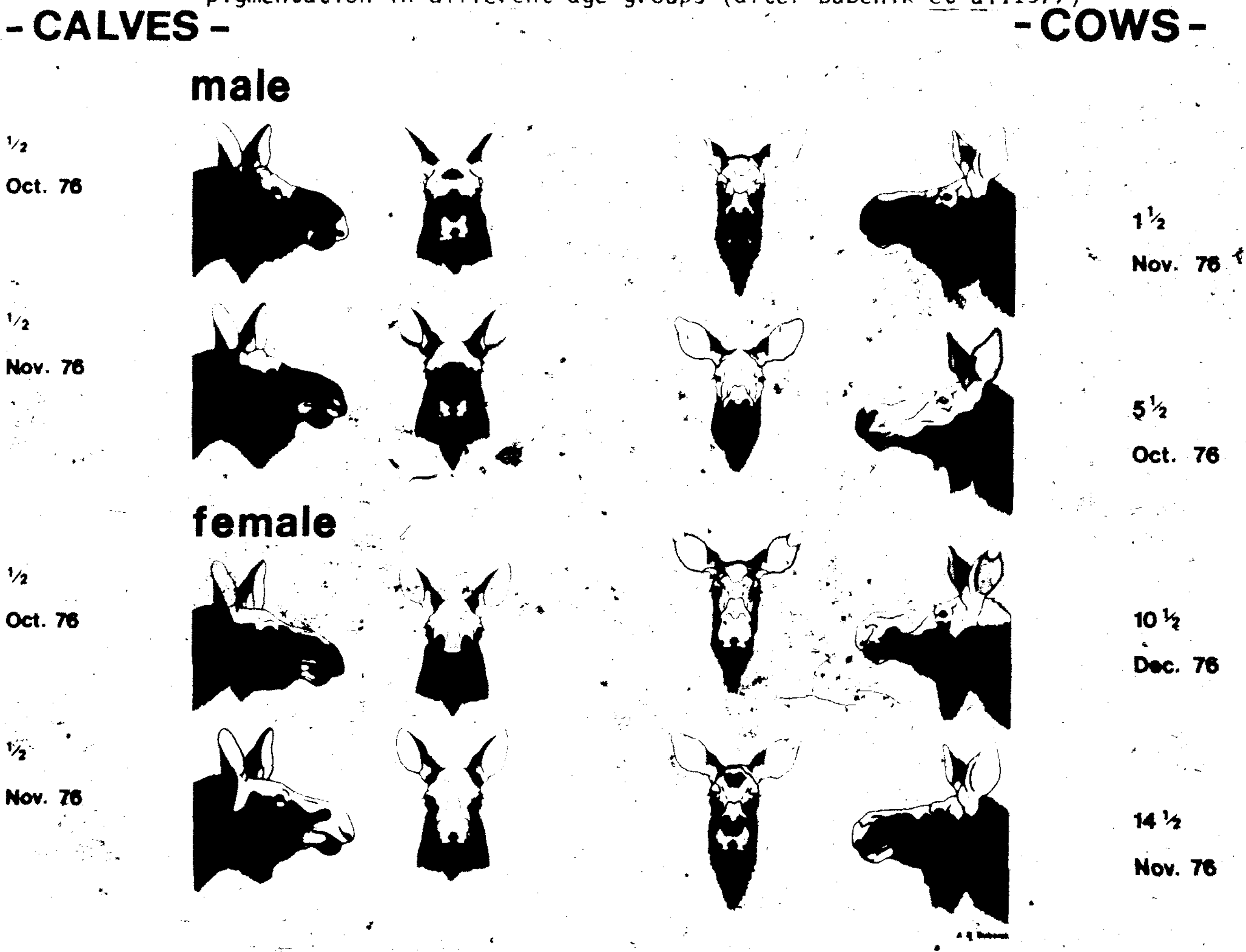
APPENDIX 1. Number of moose bells examined 1975 - 1978

*Age (yrs)	MALE Sample year 75	76	77	78	Sub total	FEMALE Sample year 75	76	77	78	Sub total	TOTAL male & female	Morphometric analysis * 1976-1977 fall period ♂	♀	Total
0.0	-	5	1	2	8	-	6	-	3	9	17			
0.3	-	-	-	1	1	-	-	-	-	-	1			
0.5	2	10	14	-	26	-	10	10	-	20	46	>24	20	44
0.8	-	2	1	-	3	-	1	-	-	1	4			
0.9	-	-	-	-	-	-	-	1	-	1	1			
1.0	-	-	5	2	7	-	-	-	2	2	9			
1.1	-	2	-	-	2	-	-	-	1	1	3			
1.5	5	26	32	-	63	2	15	35	-	52	115	>58	50	108
1.8	-	-	-	-	-	-	-	2	1	3	3			
2.0	-	-	2	-	2	-	-	-	-	-	2			
2.5	2	14	16	3	35	-	6	14	-	20	55	>30	20	50
3.0	-	-	-	-	-	-	2	-	1	3	3			
3.5	3	8	18	6	35	1	3	8	-	12	47	>26	11	37
4.0	-	-	-	-	-	-	-	1	-	1	1			
4.5	-	3	4	1	8	1	7	6	-	14	22	> 7	13	20
4.9	-	-	-	-	-	-	-	1	-	1	1			
5.0	-	-	1	-	1	-	1	-	-	1	2			
5.5	-	5	4	1	10	-	3	3	-	6	16	>20	15	35
6.5	-	8	3	-	11	-	2	7	-	9	20			
7.0	-	-	-	-	-	-	-	-	1	1	1			
7.1	-	-	-	1	1	-	-	-	-	-	1			
7.5	-	2	-	4	6	-	1	8	-	9	15			
7.8	-	-	-	-	-	-	-	-	1	1	1	> 4	9	13
8.5	2	1	1	-	4	1	-	-	-	1	5			
9.0	-	-	-	-	-	-	1	-	-	1	1			
9.5	-	1	1	-	2	-	3	3	-	6	8			
10.5	-	-	2	2	4	-	1	-	-	1	5			
10.9	-	-	-	-	-	-	-	1	-	1	1			
11.5	-	-	1	1	2	-	1	-	-	1	3	> 8	23	31
12.5	-	-	2	-	2	-	2	4	-	6	8			
13.0	-	-	-	-	-	-	1	-	-	1	1			
13.5	-	-	-	-	-	-	1	1	-	2	2			
14.5	-	-	1	-	1	-	1	1	-	2	3			
15.5	-	-	-	1	1	-	2	1	-	3	4			
Total					235					192	427	177	161	338

NOTE: *Kill time period - 0.0, 1.0, 2.0, 3.0, 4.0, 5.0, 7.0, 9.0, 13.0 - May 15-June15
1.1, 7.1 - June-July; 0.3-August; 0.5, 1.5, 2.5, 3.5, 4.5, (5.5-6.5), (7.5-8.5),
9.5+ - October 4 - December 15; 0.8, 1.8, 7.8 - January-February; 0.9, 4.9,
10.9 - March - April

Appendix 2 Selected profiles of moose showing bell development and degree of pigmentation in different age groups (after Bubenik et al. 1977)

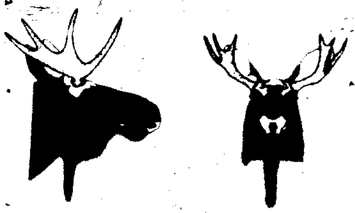


Appendix 2 continued

-BULLS-

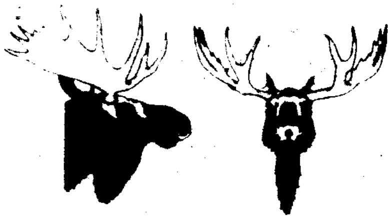

1½
Oct. 76


2½
Oct. 76


3½
Oct. 76


4½
Oct. 76

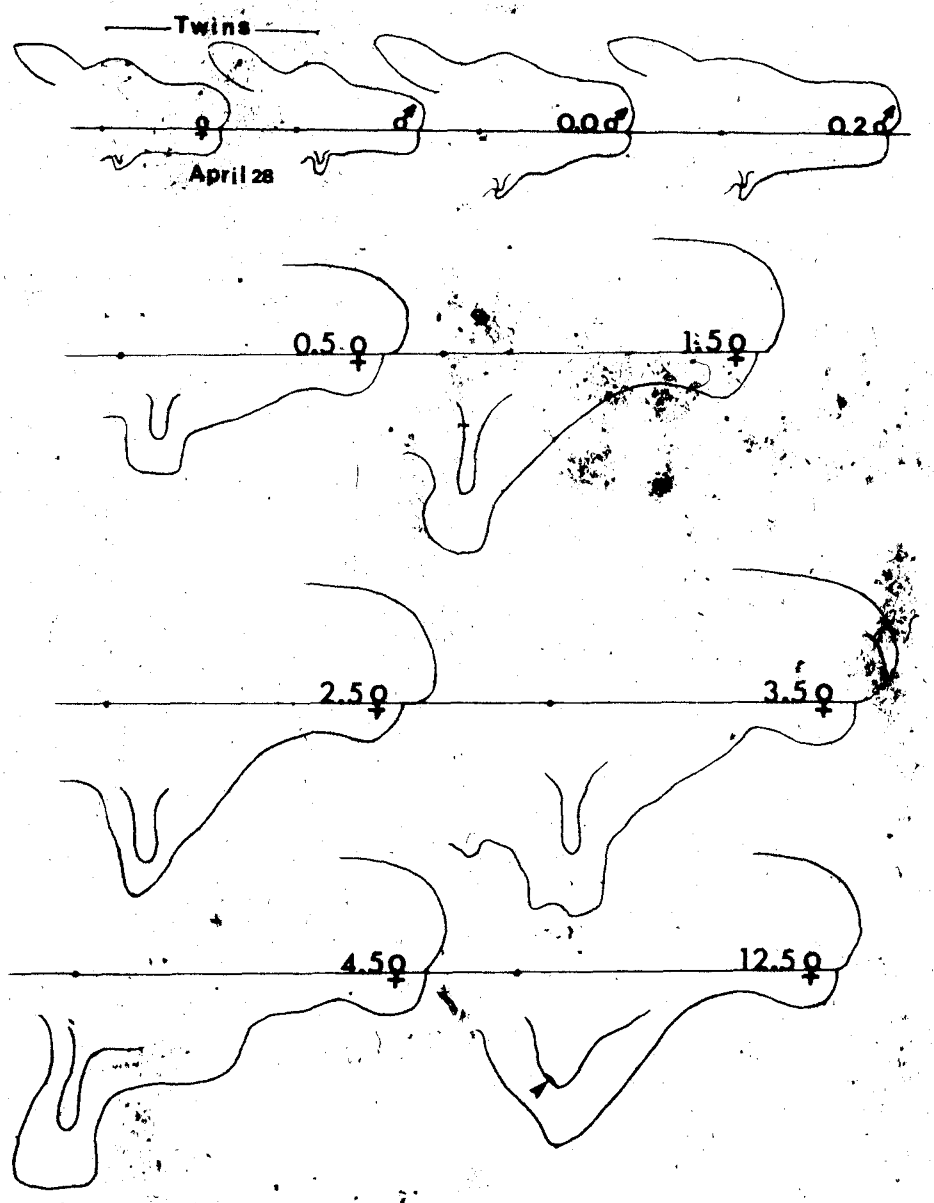

5½
Oct. 76


7½
Dec. 76


9½
Dec. 76

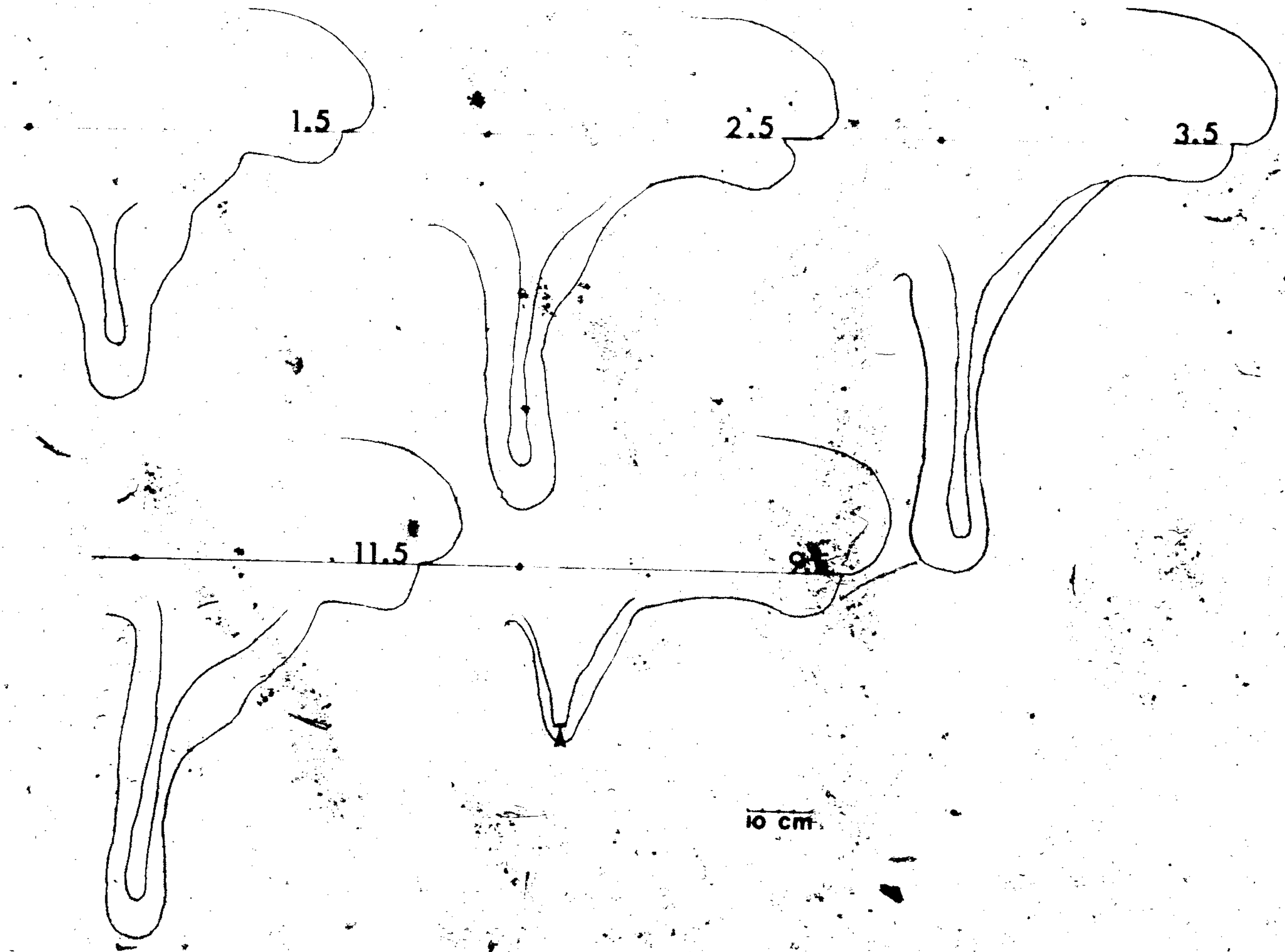

10½
Oct. 76

Appendix 3. Bell profiles drawn with and without hair from selected animals.

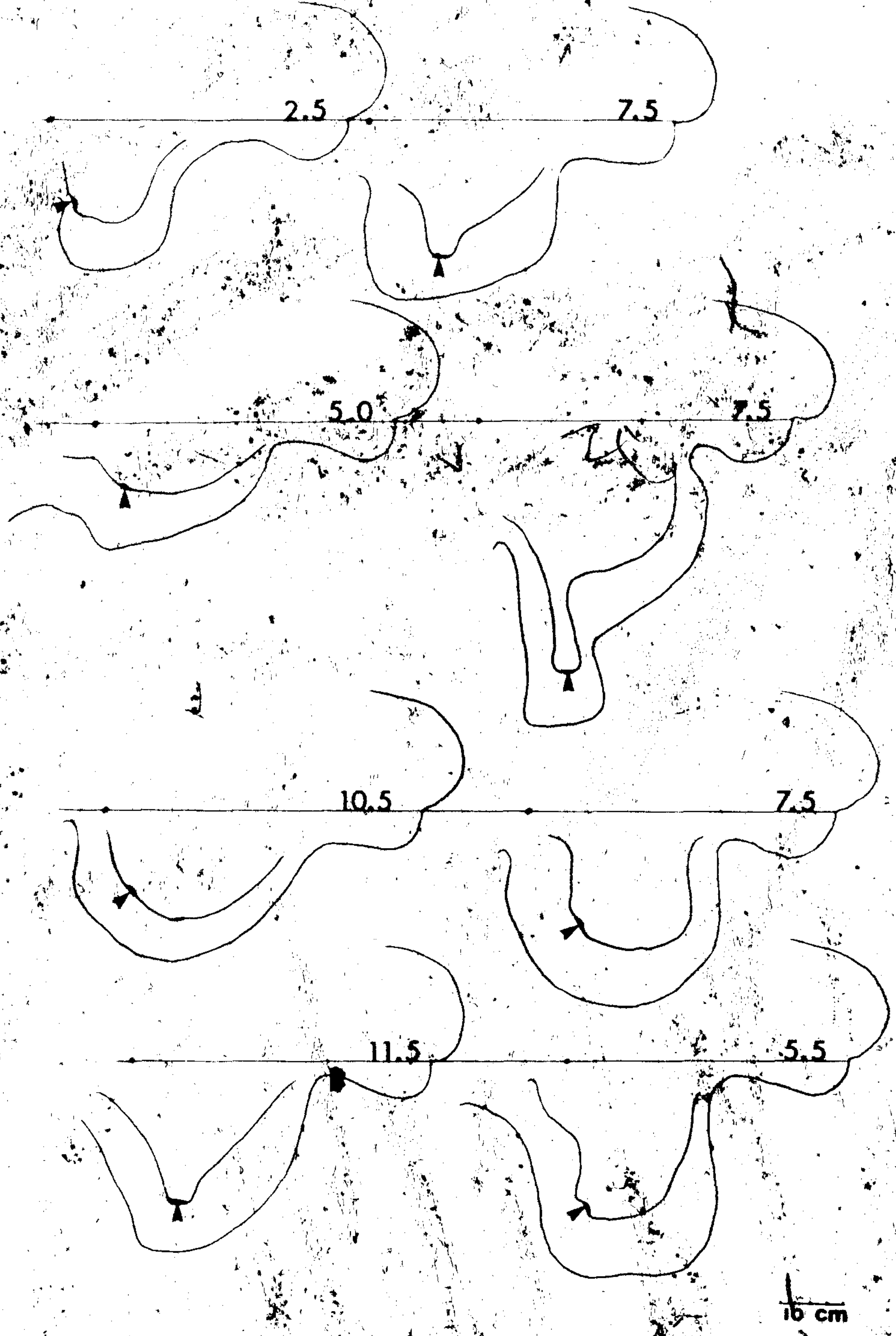


▲ indicates location of terminal scar

Appendix 3 (Cont'd) ♂♂



Appendix 3 (Cont'd) ♂♂



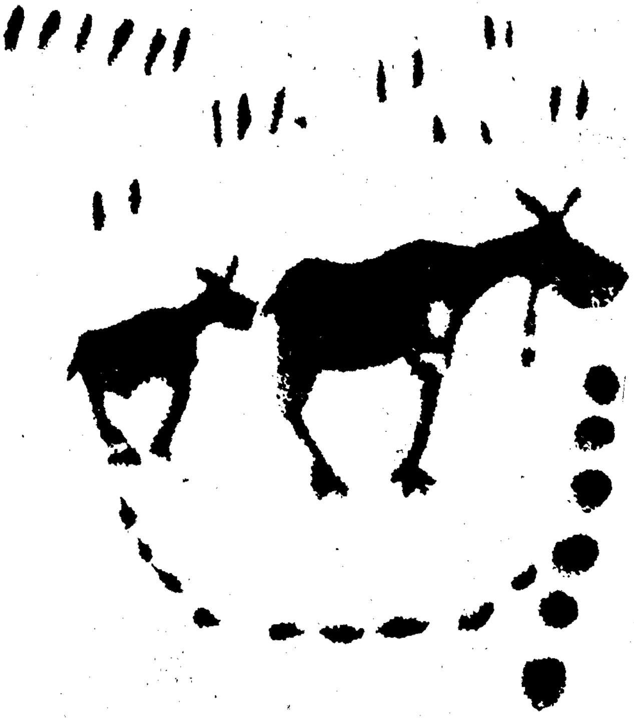
APPENDIX Number of ticks (*D. albipictus*) counted on 22 male bells

Age (yrs)	Time Killed			Bell tail surface area (cm^2)		Number nymphs (density/cm^2)		Number	
	Date	Mo.	Yr.	Proximal	Distal	Proximal	Distal	Larvae	Adults
0.5	11	10	77	33.2	21.0	0 (0.0)	0 (0.0)	-	-
	29	10	77	110.2	33.8	21 (0.19)	113 (3.34)	-	1♂
	13	11	77	25.8	20.6	110 (3.91)	225 (10.92)	-	-
	14	11	77	34.8	29.0	6 (0.17)	23 (0.79)	1	-
1.5	26	10	77	67.4	27.4	14 (0.21)	30 (1.09)	-	-
	28	10	77	194.2	44.4	3 (0.02)	4 (0.09)	-	-
	3	11	77	128.3	47.4	39 (0.30)	33 (0.70)	-	-
	6	11	77	50.6	38.4	54 (1.07)	22 (5.76)	12	-
	12	11	77	121.2	54.2	44 (0.36)	100 (1.85)	1	1♀
	27	11	77	83.2	29.2	43 (0,52)	35 (1.20)	-	1♂
	12	12	77	48.8	28.8	7 (0.14)	15 (0.52)	-	-
2.5	22	10	77	89.6	45.6	16 (0.18)	18 (0.39)	-	1♂
	11	11	77	242.8	52.8	60 (0.25)	42 (0.80)	-	1♂
	28	11	77	190.6	50.4	203 (1.07)	186 (3.69)	-	-
3.5	15	10	77	154.6	55.6	88 (0.57)	71 (1.28)	17	-
4.5	26	10	77	292.4	76.2	49 (0.17)	33 (0.43)	-	-
5.5	17	11	77	180.4	56.0	59 (0.31)	92 (1.64)	1	-
	19	11	77	357.4	35.6	256 (0.72)	123 (3.46)	-	-
6.5	30	10	77	53.6	49.8	13 (0.24)	24 (0.48)	-	-
7.5	19	11	77	61.4	28.2	29 (0.47)	36 (1.28)	-	-
9.5	11	10	77	79.4	49.4	1 (0.01)	2 (0.04)	-	-
	13	10	77	110.6	56.2	1 (0.01)	4 (0.07)	-	-
Total				2710.4	930.0	1116 (0.41)	1231 (1.32)	32	4♂,1♀

APPENDIX 5 Number of ticks (*D. albipictus*) counted on 32 female bells

Age (yrs)	Time Killed Date	Mo.	Yr.	Bell tail surface area (cm^2) Proximal	Distal	Number nymphs (density/cm^2) Proximal	Distal	Number Larvae	Adults
0.5	29	10	77	38.2	8.4	1 (0.03)	0 (0.0)	-	-
	03*	12	76	46.0	13.8	33 (0.72)	88 (13.8)	-	-
	03*	12	76	40.4	22.1	37 (0.92)	96 (22.1)	1	-
1.5	16	10	77	225.2	52.2	6 (0.03)	4 (0.08)	-	-
	22	10	77	61.4	24.8	2 (0.03)	15 (0.60)	2	-
	1	11	77	67.8	29.8	9 (0.13)	54 (1.81)	1	-
	5	11	77	41.0	22.6	10 (0.24)	55 (2.43)	-	-
	26	11	77	116.8	41.8	30 (0.26)	8 (0.19)	-	-
	27	11	77	49.8	40.4	1 (0.02)	7 (0.17)	-	-
	6	12	76	55.2	23.4	143 (2.59)	178 (7.61)	-	1♂
	6	12	77	41.4	17.2	3 (0.07)	32 (1.86)	-	-
2.5	20	10	77	31.8	22.0	0 (0.0)	1 (0.05)	-	-
	6	11	77	18.0	19.0	5 (0.28)	23 (1.21)	-	-
	11	11	77	72.2	40.6	1 (0.01)	10 (0.25)	-	-
	[illegible]	10	77	89.6	33.4	0 (0.0)	0 (0.0)	-	-
3.5	11	10	77	108.4	25.4	1 (0.01)	1 (0.04)	-	-
4.5	12	10	77	131.2	32.2	0 (0.0)	0 (0.0)	-	-
5.5	13	10	77	120.8	46.8	64 (0.53)	42 (0.90)	-	-
	22	10	77	92.4	31.4	8 (0.09)	17 (0.54)	-	1♂
	22	10	77	94.4	44.0	2 (0.02)	2 (0.05)	-	-
	12	11	77	81.0	40.4	5 (0.06)	5 (0.12)	-	-
	27	11	77	39.8	32.8	14 (0.35)	41 (1.25)	-	-
	29	11	77	38.6	21.6	24 (0.62)	41 (1.90)	-	-
6.5	13	11	77	70.6	29.8	11 (0.16)	20 (0.67)	-	-
7.5	16	11	77	57.0	38.0	36 (0.63)	98 (2.58)	3	-
8.5	27	11	77	94.6	31.6	8 (0.08)	17 (0.54)	-	-
	27	11	77	51.6	27.4	9 (0.17)	36 (1.31)	-	-
	2	12	77	70.8	30.6	4 (0.06)	15 (0.49)	-	-
9.5+	28	10	77	69.6	31.6	65 (0.93)	95 (3.01)	2	-
	3*	12	76	188.4	42.0	47 (0.25)	81 (1.93)	-	-
	6	12	77	33.0	22.0	7 (0.21)	9 (0.41)	-	-
	15	12	77	122.2	30.6	8 (0.07)	13 (0.42)	-	-
Total				2459.2	969.7	594 (0.24)	1104 (1.14)	9	2♂

* twin calves and female



Frontise and Backpiece

from

Dewdney and Kidd 1967