

# Studies of morphological parameters affecting ungulate locomotion in snow

EDMUND S. TELFER

Canadian Wildlife Service, 9942 - 108 Street, Edmonton, Alta., Canada

AND

JOHN P. KELSALL

Canadian Wildlife Service, P.O. Box 340, Delta, B.C., Canada

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We deal with possible morphological adaption to varied snow conditions by four North American ungulate species. Chest heights and weight loads on track are key parameters in estimating capabilities of species, and of age and sex classes within species, to cope with snow. Methods believed suitable for measuring those parameters in replicable fashion are discussed. Comparative studies of bison (*Bison bison*), moose (*Alces alces*), wapiti (*Cervus elaphus*), and white-tailed deer (*Odocoileus virginianus*) are described. There are pronounced differences in both parameters between species and between some age and sex classes within species. Chest heights of the three cervids differed by a fixed interval suggesting that differential ability to use varied snow depths may play a role in resource partitioning. Differential winter mortality may be related to sex and age class differences in ability to cope with snow. Morphological differences relate to regional distributions by determining species suitability for survival in varying snow regimes.

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Il est possible que les conditions apportées par la neige aient entraîné des adaptations morphologiques chez quatre espèces nord-américaines d'ongulés. La hauteur du poitrail et la pression de la masse sur la neige sont les principaux paramètres qui servent à estimer la facilité d'une espèce et des différentes classes d'âge et de sexe à vivre dans la neige. Certaines méthodes semblent plus que d'autres susceptibles de mesurer adéquatement et fidèlement les paramètres. On trouvera ici les résultats d'une étude sur le bison (*Bison bison*), l'orignal (*Alces alces*), le wapiti (*Cervus elaphus*) et le cerf à queue blanche (*Odocoileus virginianus*). Les deux paramètres diffèrent selon l'espèce et parfois selon les classes d'âge et de sexe chez une même espèce. Il y a un intervalle fixe entre les hauteurs de poitrail des trois cervidés; les trois espèces utilisent donc des profondeurs de neige différentes, ce qui contribue sans doute à la séparation des ressources. La mortalité différentielle en hiver peut être associée à la capacité différentielle des animaux de vivre dans la neige selon leur sexe ou leur classe d'âge. Les différences morphologiques affectent les répartitions régionales en influençant la capacité de survie des espèces à diverses conditions nivales.

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## Introduction

In recent years there has been increasing interest in snow as a factor in the ecology of animals in North America. Much of the work was stimulated by the Russians Formozov (1946) and Nasimovich (1955). Among the large ungulates, North American populations of moose, white-tailed deer, mule deer (*Odocoileus hemionus*), barren-ground caribou (*Rangifer tarandus*), bison, and muskox (*Ovibos moschatus*), have been the subjects of study by Pruitt (1959), Des Meules (1964), Telfer (1967, 1970), Kelsall (1968, 1969), Verme (1968), Ozoga (1968), Gilbert *et al.* (1970), Lent and Knutson (1971), Peek (1971), Kelsall and Prescott (1971), Meagher (1973), Peterson and Allen (1974), Coady (1974), Van Camp (1975), and others.

External morphology and behavior reflect adap-

tion to snow. Variation in those adaptations are reflected in different abilities of mammals to survive in snow and exist between species and between age and sex classes within species. We believe that many of those differences are explicable in simple morphological terms (Kelsall and Telfer 1971). We have examined structural parameters, and developed replicable techniques for their measurements, for four species of large western Canadian mammals. The parameters are chest heights, which indicate the ability of large mammals to cope with snow of varying thickness, and foot and hoof loads, which indicate their ability to cope with snow of varying density and hardness. Although density and hardness of snow are poorly correlated (Gold 1956) both characteristics provide support to ungulates (Pruitt 1959; Kelsall and Prescott 1971).

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A particular concern has been measurements of weight load on track, derived by dividing live weight of a mammal by total area of its four feet. In the case of ungulates, we have differentiated between hoof load, which is the weight load on the hoof alone, and foot load, which is the weight load on the entire foot from dewclaws to the tip of hoof. Hoof loads have been used in the literature (Nasimovich 1955; Kelsall 1969), but foot loads seem a more realistic measurement since the whole hoof-pastern-dewclaw area offers support in snow. Also, measurements of foot area can, we think, be systematic and objective, while that of hooves alone is necessarily more subjective because of the way in which the posterior end of each toe sweeps upward from the horizontal.

This paper describes our measurements and compares four species of ungulates, and age and sex classes within species. Those species (bison, moose, wapiti or American elk, and white-tailed deer) offer contrasts in morphological adaption to snow. They may all be found occupying the same general areas, as in Elk Island National Park, Alberta, but appear to fill somewhat different ecological niches and occupy different winter ranges.

## Materials and Methods

### Field Procedures

Reduction slaughters in Elk Island and Jasper National parks provided us with study material. The following mammals were collected: 146 moose, 100 wapiti and 93 white-tailed deer in Elk Island National Park between December 1 and 17, 1969; 122 wapiti taken in Jasper National Park between December 17, 1969, and February 6, 1970; and 153 bison from Elk Island National Park, most of the males being taken in the first week in December, 1969, and most of the females in the first 2 weeks in December, 1971.

Elk Island National Park is situated in the southern fringe of the boreal mixed wood forest (Rowe 1972) and is characterized by aspen (*Populus tremuloides*) stands. Jasper wapiti winter in montane (Rowe 1972) vegetation but summer in adjacent subalpine forest. Both areas provide good to excellent winter range. The bison belong to the plains form (*Bison bison bison*) introduced from Montana in 1908. Elk in Jasper descend from a mixed population of native animals and others introduced from Yellowstone National Park ca. 1916.

We obtained carcass weights and measurements including chest heights from whole, freshly killed animals. "Chest height" is the shortest distance from the distal tip of the front hoof to the midline of the brisket, with the front leg fully extended perpendicular to the body (Kelsall 1969). It is thus slightly greater than the chest height of a standing animal, but has the advantage of being a simply made and replicable measurement. The lower part of all four legs with feet attached were collected from each animal during butchering, placed in a burlap bag, appropriately labelled and frozen until laboratory examination. Lower jaws were also collected for later determination of ages of the older cervids. Ages of bison were all determined from records of the ear tags that each animal carried.

### Laboratory Procedures

Each hoof from each mammal was measured as follows: (1) Foot lengths, from the distal ends of the toes to the proximal

ends of the dewclaws, were taken by flexing each thawed foot and placing it against a back board on a sheet of graduated paper (Fig. 1). (2) Hoof outlines were obtained by inking each on a large stamp pad and then stamping an outline on paper. Each outline, which was always discontinuous, was enclosed by a penciled line around the outside of the ink marks, and the back of the hoof was enclosed by a straight line joining the posterior tips of the imprints of the toes (Fig. 2). (3) The hoof area was obtained with a planimeter as the sum of two parts; (A) distal to a line across the widest part of the hoof and (B) posterior to that line (Fig. 2). (4) The total foot area was estimated by adding to the area of the distal part of the hoof ((A) above) the area of a rectangle which equalled (total foot length - distance 'A') × hoof width (Fig. 2).

The precision of this method was tested by 26 staff members, some of whom had never made biological measurements. Using the same set of hooves, they measured foot lengths, then stamped and outlined a hoof from each of a bison, moose, wapiti, and white-tailed deer.

We explored a number of possibilities for the determination of foot area by a simpler and more direct means than that outlined above. Of various parameters examined, only the index (foot length × hoof width) appears to provide a good positive correlation with foot area. Although the technique has not been tested extensively, it is apparent that good estimates of foot area could be indirectly obtainable from simple measurements made on even whole animals in the field.

Hoof and foot loads were calculated for each animal by dividing whole carcass weights by the combined area for all four hooves or feet.

Where necessary, ages of animals were determined from growth layers in dental cement as per Sargeant and Pimlott (1959) and Mitchell (1967).

Our use of scientific nomenclature for mammals follows Banfield (1974).

## Results

### Accuracy of Measurement Techniques

Data relating to tests of the precision of the methods of estimating hoof and foot areas was presented by Kelsall and Telfer (1971). It showed that our 26 observers, some of whom were skilled at making measurements and some of whom were not, came within 4.5% of the mean 95% of the time. Variability in the results was greatest for white-tailed deer and least for moose. From those results,

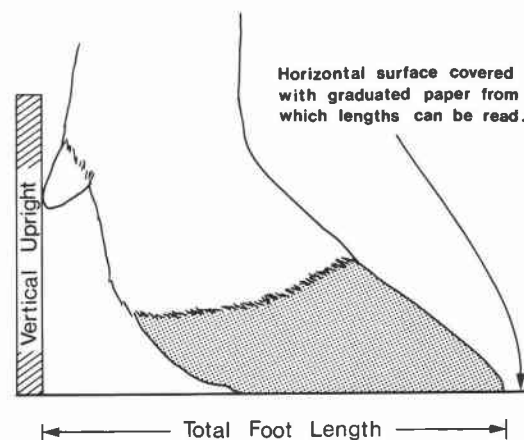


FIG. 1. A method for measuring total foot length of ungulates.

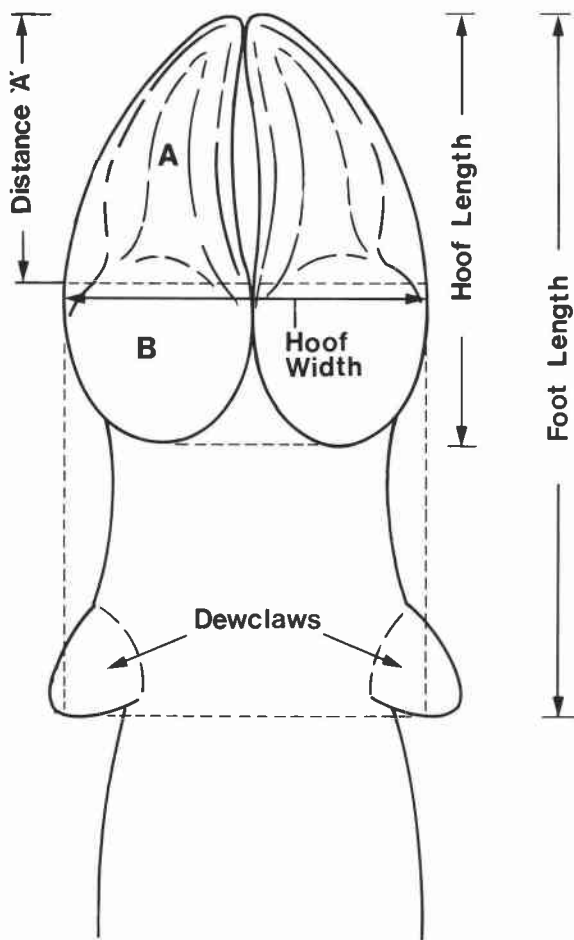


FIG. 2. A diagram of an ungulate foot showing foot and hoof lengths and hoof outline. Total foot area is obtained by adding the area of the front part of the hoof (A) to the area of the rectangle: (foot length - distance 'A')  $\times$  hoof width B.

and from our own observations, it seems that, because of their smaller feet, errors in measurements of hooves of white-tailed deer form a greater percentage of the total.

#### Differences Between Wapiti Populations

We examined the possibility of quantitative differences between wapiti taken in Elk Island National Park and Jasper National Park. The two populations were compared (Kelsall and Telfer 1971). The only statistically significant differences were in live weight in 2 of 10 age and sex categories. Those differences influenced hoof load measurements, but not to the extent where they were significantly different between populations. Our conclusion was that the heavier animals, from Jasper National Park, were simply in better nutritional condition and that such minor differences could be ignored. For purposes of this paper,

therefore, data from the two populations have been combined.

#### Chest Heights

Where there are statistically adequate sample numbers, chest height increases with age as would be expected (Tables 1-4). The increase is continuous up to the age of  $4\frac{1}{2}$  years with elk and moose. Both white-tailed deer and bison appear to achieve adult chest height at an earlier age. However, our samples from young and female bison are inadequate.

TABLE 1. Chest heights, in centimetres, of white-tailed deer by sex and age class. The  $4\frac{1}{2}$  year age class in this and following tables includes animals of that age and older

| Sex    | Age            | No. | Range     | Mean $\pm$ SE |
|--------|----------------|-----|-----------|---------------|
| Male   | $\frac{1}{2}$  | 6   | 45.1-55.2 | 50.5 1.33     |
|        | $1\frac{1}{2}$ | 10  | 56.5-67.9 | 62.1 1.15     |
|        | $2\frac{1}{2}$ | 5   | 59.7-66.0 | 62.9 1.05     |
|        | $3\frac{1}{2}$ | 7   | 57.8-68.6 | 63.9 1.46     |
|        | $4\frac{1}{2}$ | 11  | 58.4-67.3 | 63.8 0.75     |
| Female | $\frac{1}{2}$  | 14  | 44.6-56.5 | 49.7 0.94     |
|        | $1\frac{1}{2}$ | 13  | 53.3-63.5 | 57.0 0.86     |
|        | $2\frac{1}{2}$ | 11  | 55.9-67.9 | 59.7 1.05     |
|        | $3\frac{1}{2}$ | 6   | 54.6-63.5 | 57.6 1.34     |
|        | $4\frac{1}{2}$ | 10  | 52.1-63.5 | 58.0 1.07     |

TABLE 2. Chest heights of wapiti by age and sex class. In this and other tables and figures, standard errors of the mean and standard deviations are not given where sample size is four animals or less

| Sex    | Age            | No. | Range     | Mean $\pm$ SE |
|--------|----------------|-----|-----------|---------------|
| Male   | $\frac{1}{2}$  | 18  | 64.8-86.4 | 75.8 1.63     |
|        | $1\frac{1}{2}$ | 11  | 73.7-86.4 | 80.9 0.96     |
|        | $2\frac{1}{2}$ | 9   | 84.5-94.0 | 88.9 0.89     |
|        | $3\frac{1}{2}$ | 4   | 80.0-94.0 | 86.2 —        |
|        | $4\frac{1}{2}$ | 32  | 78.7-95.3 | 88.7 0.66     |
| Female | $\frac{1}{2}$  | 12  | 76.2-94.0 | 76.2 1.28     |
|        | $1\frac{1}{2}$ | 20  | 71.1-91.4 | 80.9 1.32     |
|        | $2\frac{1}{2}$ | 18  | 76.8-91.4 | 83.1 1.01     |
|        | $3\frac{1}{2}$ | 14  | 78.1-91.4 | 83.5 0.80     |
|        | $4\frac{1}{2}$ | 83  | 76.2-94.0 | 83.4 0.41     |

TABLE 3. Chest heights of moose by age and sex class

| Sex    | Age            | No. | Range       | Mean $\pm$ SE |
|--------|----------------|-----|-------------|---------------|
| Male   | $\frac{1}{2}$  | 12  | 77.5- 94.0  | 87.8 1.41     |
|        | $1\frac{1}{2}$ | 4   | 96.5-100.3  | 98.8 —        |
|        | $2\frac{1}{2}$ | 5   | 96.5-107.3  | 103.2 1.84    |
|        | $3\frac{1}{2}$ | 13  | 101.6-110.5 | 106.4 0.75    |
|        | $4\frac{1}{2}$ | 37  | 101.6-111.8 | 106.6 0.50    |
| Female | $\frac{1}{2}$  | 7   | 86.4- 95.3  | 89.4 1.13     |
|        | $1\frac{1}{2}$ | 4   | 96.5-108.0  | 101.6 —       |
|        | $2\frac{1}{2}$ | 12  | 97.8-108.6  | 102.8 0.91    |
|        | $3\frac{1}{2}$ | 9   | 95.3-108.0  | 103.0 1.50    |
|        | $4\frac{1}{2}$ | 39  | 94.6-111.8  | 105.2 0.59    |

TABLE 4. Chest heights of bison by age and sex class

| Sex    | Age | No. | Range     | Mean ± SE |
|--------|-----|-----|-----------|-----------|
| Male   | ½   | 2   | —         | 63.5      |
|        | 1½  | 1   | —         | 66.0      |
|        | 2½  | 16  | 63.5–76.2 | 71.0 0.96 |
|        | 3½  | 12  | 64.8–74.9 | 68.6 0.77 |
|        | 4½  | 95  | 59.7–76.2 | 67.7 0.33 |
| Female | ½   | 2   | 57.2–61.0 | 59.1      |
|        | 1½  | 1   | —         | 50.8      |
|        | 2½  | —   | —         | —         |
|        | 3½  | 2   | 63.0–66.5 | 64.8      |
|        | 4½  | 23  | 55.9–69.9 | 64.3 0.70 |

Sexes within species appear to have approximately equal chest heights during the first year or year and a half of life but diverge with age. Although our data are not always consistent, males ultimately grow taller. The inconsistencies are probably due to inadequate sample sizes. Mean chest heights for males older than 4½ years are invariably greater than those for females of the species and of the same age, and differences are statistically significant except for moose (Fig. 3). Ranges between male and female measurements within species invariably overlap, so that it can fairly be said that the biological significance of difference between sexes is not nearly as great as the statistical significance.

Foot Loading

Like chest height, foot loads of the various species increase with advancing age, with the males becoming progressively heavier on their feet than the females (Tables 5–8). Foot loadings for wapiti, moose, and bison increase up to 4½ years of age at least. Differences between age groups are more marked in males than in females. Those differences are doubtless related to the increase in size and weight of horns and antlers carried by the males, and increasingly heavy configuration of the shoulders, neck, and head with advancing age up to sexual maturity (Fig. 4).

Differential in Hoof Area

In earlier publications (e.g. Kelsall 1968) it was suggested that the area of front hooves tends to be greater than rear hooves. That parameter was measured among many of our samples, for all four species (Table 9). Mean values for hoof area are consistently greater for front hooves than for rear hooves. In the cases of moose, wapiti and bison the differences for both sexes are significantly different ( $p \leq 0.05$ ). The percent difference in mean values is consistently greater for males than for females. As with foot loads, the difference may be an adaption for the support of the heavy antlers or horns and

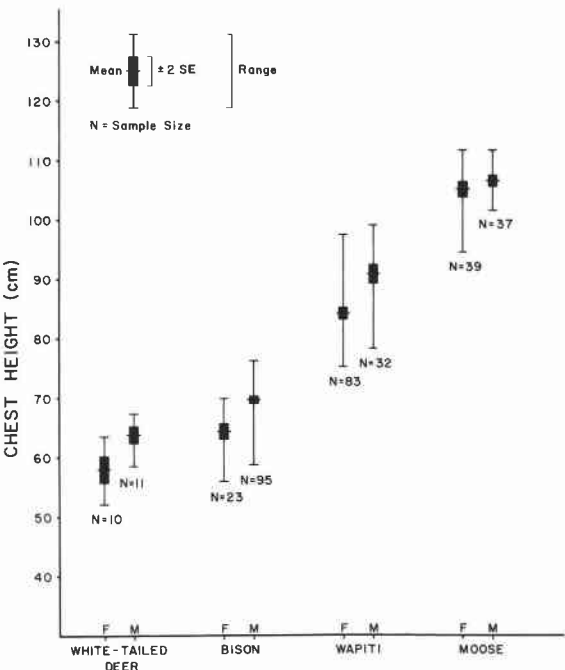


FIG. 3. Chest heights of males and females over 4½ years old belonging to four ungulate species.

TABLE 5. Foot loads, in grams per square centimetre, for white-tailed deer, by sex and age class

| Sex    | Age | No. | Range       | Mean ± SE   |
|--------|-----|-----|-------------|-------------|
| Male   | ½   | 6   | 239.7–360.8 | 287.8 18.09 |
|        | 1½  | 10  | 358.0–511.8 | 412.5 14.94 |
|        | 2½  | 5   | 490.7–575.8 | 536.1 17.61 |
|        | 3½  | 7   | 466.5–591.0 | 519.5 18.99 |
|        | 4½  | 11  | 439.9–602.1 | 512.0 13.28 |
| Female | ½   | 14  | 255.6–274.8 | 327.5 9.17  |
|        | 1½  | 13  | 263.1–500.3 | 427.7 11.52 |
|        | 2½  | 11  | 374.9–567.8 | 467.1 18.03 |
|        | 3½  | 6   | 396.3–556.0 | 474.3 24.78 |
|        | 4½  | 10  | 374.1–564.7 | 474.3 20.00 |

TABLE 6. Foot loads, in grams per square centimetre, for wapiti by sex and age class

| Sex    | Age | No. | Range       | Mean ± SE   |
|--------|-----|-----|-------------|-------------|
| Male   | ½   | 18  | 329.3–630.5 | 457.7 18.26 |
|        | 1½  | 12  | 494.2–649.1 | 544.5 14.43 |
|        | 2½  | 7   | 535.1–691.3 | 624.7 18.08 |
|        | 3½  | 4   | 668.5–806.6 | 721.2 —     |
|        | 4½  | 33  | 532.2–864.2 | 737.6 12.52 |
| Female | ½   | 12  | 379.8–590.4 | 481.9 17.30 |
|        | 1½  | 20  | 454.2–641.4 | 541.8 11.11 |
|        | 2½  | 18  | 509.8–751.6 | 606.9 13.69 |
|        | 3½  | 14  | 512.6–767.6 | 615.5 18.16 |
|        | 4½  | 84  | 486.7–753.1 | 641.3 5.94  |

TABLE 7. Foot loads, in grams per square centimetre, for moose by sex and age class

| Sex    | Age            | No. | Range       | Mean $\pm$ SE |
|--------|----------------|-----|-------------|---------------|
| Male   | $\frac{1}{2}$  | 12  | 313.5–440.8 | 396.8 11.20   |
|        | $1\frac{1}{2}$ | 4   | 464.2–541.2 | 487.3 —       |
|        | $2\frac{1}{2}$ | 5   | 489.1–691.8 | 553.4 37.00   |
|        | $3\frac{1}{2}$ | 13  | 475.6–727.8 | 622.8 20.94   |
|        | $4\frac{1}{2}$ | 38  | 559.8–836.1 | 658.8 12.20   |
| Female | $\frac{1}{2}$  | 7   | 369.9–401.9 | 389.5 5.35    |
|        | $1\frac{1}{2}$ | 4   | 423.5–498.0 | 475.7 —       |
|        | $2\frac{1}{2}$ | 12  | 473.3–730.3 | 558.3 18.41   |
|        | $3\frac{1}{2}$ | 12  | 462.2–716.5 | 591.7 21.80   |
|        | $4\frac{1}{2}$ | 38  | 539.0–835.9 | 629.4 12.00   |

TABLE 8. Foot loads, in grams per square centimetre, for bison by sex and age class

| Sex    | Age            | No. | Range        | Mean $\pm$ SE |
|--------|----------------|-----|--------------|---------------|
| Male   | $\frac{1}{2}$  | 2   | 425.8–625.8  | 525.8 —       |
|        | $1\frac{1}{2}$ | 1   | —            | 599.1 —       |
|        | $2\frac{1}{2}$ | 16  | 615.9–882.6  | 704.2 18.95   |
|        | $3\frac{1}{2}$ | 12  | 570.0–927.9  | 776.1 31.57   |
|        | $4\frac{1}{2}$ | 91  | 617.7–1025.9 | 884.1 8.02    |
| Female | $\frac{1}{2}$  | 2   | 508.7–584.5  | 546.6 —       |
|        | $1\frac{1}{2}$ | 1   | —            | 545.8 —       |
|        | $2\frac{1}{2}$ | —   | —            | —             |
|        | $3\frac{1}{2}$ | 2   | 541.6–759.1  | 650.4 —       |
|        | $4\frac{1}{2}$ | 22  | 576.1–784.8  | 672.4 9.47    |

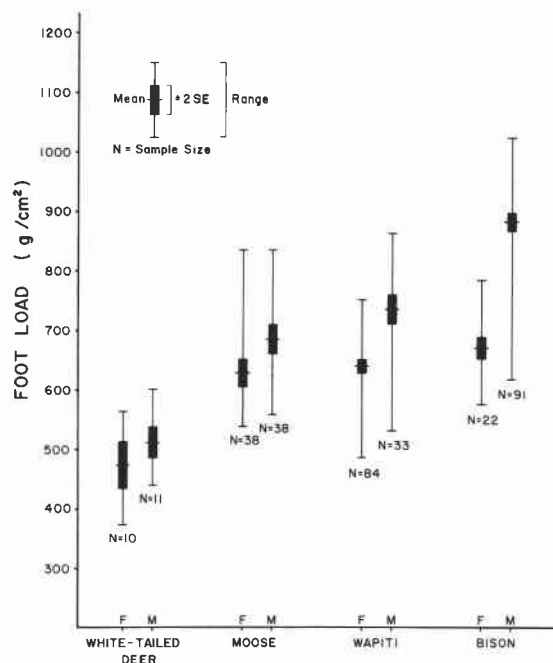
more massive male neck and forequarters although we have no data to support this view.

White-tailed deer present a slightly different picture (Table 9). Mean values for front hooves is 9.7% greater than for rear hooves among male animals. In that case, however, judging from the mean values and their standard errors, the difference is barely significant at the 95% confidence level. Although the mean value for front hooves is slightly larger than that for rear hooves among female white-tailed deer, the difference is not statistically significant.

The statistics for white-tailed deer may be deceptive because of small sample size, and hoof area relationships may actually be similar to those demonstrated for the other three species.

### Discussion

Separation in chest heights of fully mature ( $4\frac{1}{2}$  years) deer, wapiti, and moose was remarkably uniform (Fig. 4). Deer were approximately 24 cm shorter than wapiti, and the latter were 22 cm shorter than moose. Because the three cervids can all survive on browse once deep snow arrives the separation in chest heights might permit differential utilization of areas with varied snow cover thicknesses. Snow covers of different thickness

FIG. 4. Foot loading of males and females over  $4\frac{1}{2}$  years old belonging to four ungulate species.TABLE 9. Comparison of areas of front and hind hoofs, in square centimetres, for four species of ungulates  $4\frac{1}{2}$  years of age or older

| Species           | Sex    | No. | Hoof area      |      |               |     | % differences |
|-------------------|--------|-----|----------------|------|---------------|-----|---------------|
|                   |        |     | Front $\pm$ SE |      | Rear $\pm$ SE |     |               |
| White-tailed deer | Male   | 22  | 21.6           | 0.5  | 19.5          | 0.6 | 9.7           |
|                   | Female | 20  | 18.4           | 0.4  | 18.1          | 0.4 | 1.6           |
| Wapiti            | Male   | 66  | 66.0           | 1.4  | 56.3          | 0.9 | 14.7          |
|                   | Female | 170 | 56.9           | 0.5  | 49.6          | 0.4 | 12.8          |
| Moose             | Male   | 78  | 97.2           | 0.9  | 88.2          | 0.9 | 9.3           |
|                   | Female | 80  | 88.8           | 0.08 | 82.1          | 0.8 | 7.5           |
| Bison             | Male   | 190 | 133.5          | 0.9  | 113.6         | 0.7 | 14.9          |
|                   | Female | 44  | 108.5          | 1.2  | 98.3          | 1.2 | 9.4           |

may recur in a mosaic of small patches where terrain and forest cover is diversified. Where such variation exists the three cervids could coexist during winter in the same locality, eating the same foods on adjacent patches of winter range if the moose stayed in snow of greater thickness.

Bison chest heights are close to those of deer but are about 19 cm less than wapiti (Fig. 3), the other species that grazes extensively in craters in soft snow. Bison and white-tailed deer adapt behaviorally to thick snow by following old trails, thus opening beaten paths (Severinghaus and Cheatum

1956; Van Camp 1975). It will be noted that they are the species with the lowest chest height.

Distribution of foot loads of mature animals showed less difference between species than in regard to chest heights (Fig. 4). Mature moose and wapiti are close together in the middle of the range. Bison appear poorly adapted to walking on snow and their historic range did not extend into regions of thick hard snow in northeastern North America where moose were widely distributed. Note, however, the great sexual dimorphism in foot loading among bison, the females having significant advantage on hard or dense snow. Historically, wapiti likewise ranged only into the fringes of the boreal forest and of the regions of thicker snow cover in eastern Canada and the United States.

With their lighter foot loading white-tailed deer have been more successful in deep snow regions than wapiti or bison, but they are much more subject to winter mortality and oscillations in distribution in such regions than are moose. It therefore appears that the ability to cope with deep snow through possession of long legs is an adaption of slightly more survival value than low foot loading. Moose have the greatest leg length but also possess a relatively low foot loading (Figs. 3, 4), suggesting a greater degree of evolutionary adaption to snow than the other ungulates.

The data show a number of significant differences between the sexes in mature animals with the exception of foot loads of deer and chest heights of moose. Chest heights of male deer and wapiti exceeded those of females by about 6 cm, possibly giving males a slight advantage in thick snow cover. On the other hand female wapiti, bison, and perhaps moose would have an advantage in snow hard enough for ungulates to walk upon or sufficiently dense to offer support.

Subadults of all species could be expected to be at a disadvantage in a thick snow cover. However, in regions where dense snow or hard crusts occur regularly younger animals might survive better than adults because of low foot loading. Bison would be an exception because they are grazers and hard snow inhibits crater excavation by calves (Van Camp 1975).

We therefore conclude that morphological adaptations to a snow cover of variable characteristics may constitute a dimension in which sympatric ungulates in central Alberta separate to share winter food resources. Interaction of morphological parameters with snow conditions may partially explain differential winter mortality in various sex and age classes of ungulates. Our findings also support the view of Formozov (1946) that adaption to

snow is a key factor governing distribution of northern mammals.

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