# RESOURCE USE BY MOOSE VERSUS SYMPATRIC DEER, WAPITI AND BISON

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Abstract: Proposals for game ranching in western Canada involve rearing mixed species assemblages of moose (Alces alces) with other native ungulates including bison (Bison bison), wapiti (Cervus elaphus canadensis), white-tailed deer (Odocoileus virginianus) and mule deer (O. hemionus) in fenced enclosures. Elk Island National Park in central Alberta is an analog for this management system. Pellet group surveys of habitat use and food habits for the winter of 1972-73 were employed with data from aerial surveys flown between 1960 and 1976 to evaluate partitioning of the resources of food, habitat and space between moose and other sympatric ungulates. Moose were found to be separated from the other ungulates largely by their selection of places to live and additionally from bison by their food habits. Further examination of spatial separation of moose from the other cervids over a range of moose population levels showed that moose occupy additional space almost at a rate proportional to their numerical increase up to a certain level, then rate of acquisition of new territory declines. At that point, population growth is partially accommodated by increased numbers of moose groups in territory already occupied and increased number of animals per group.

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In their vast circumpolar distribution, moose are sympatric with many other species of large herbivores. However, moose population densities are often low and their relation to species with similiar ecological requirements is difficult to evaluate. The question is one of practical as well as theoretical interest. In many areas of the southern boreal forest and aspen parkland regions of western Canada, the potential exists for mixed species game ranching (Telfer and Scotter 1975). In game ranching, as in most animal husbandry, animal densities are often abnormally high so potential for species interaction is greatly increased. Habitat improvement has also become a high priority with wildlife managers in the prairie provinces. The goal again is high wintering densities of cervids and this leads to population interactions.

Elk Island National Park in central Alberta has maintained large populations of moose along with wapiti, white-tailed deer, mule deer and bison in large fenced enclosures for more than 50 years. It thus provides an excellent opportunity for studying the ecological relationships of moose with other ungulates.

The objective of the present study was to determine how moose partition the major resource axes of the herbivore niche with other ungulates. The concept of niches as consisting of resource axes or dimensions along each of which the categories of a particular resource occurs in a continuum was propounded by Hutchinson (1957) and summarized by Odum (1971). Niche theory provides a useful conceptual framework for expressing differences in resource utilization by key wildlife species.

## THE STUDY AREA

Elk Island National Park is situated 40 km east of Edmonton, Alberta. It was established in 1906 as a reserve to protect wapiti. The area was periodically expanded, reaching its present size in 1957. The park now has an area of 192 $km^2$ and is divided by Highway 16 into the North Enclosure (132 $km^2$) and the Isolation Enclosure (60 $km^2$). Both subareas are fenced with Paige wire 2.4 m high to contain populations of wapiti, moose and bison. White-tailed and mule deer can enter or leave either enclosure by crawling under the fences. Human hunting has been limited to periodic herd reduction slaughters and no wolves (*Canis lupus*), black bears (*Ursus americana*) or other effective predators are present.

The park forms part of the Beaver Hills, a stagnant ice moraine characterized by knob and kettle topography with average relief of 10 to 20 m (Lang 1974). Vegetation consists of a finely interspersed mosaic of aspen forest dominated by *Populus tremuloides* and *P. balsamifera* with a dense shrub understory comprised mostly of beaked hazel (*Corylus cornuta*); shrublands dominated by *Populus tremuloides*, *P. balsamifera* and *Betula papyrifera* saplings, willows (*Salix* spp.), saskatoon (*Amelanchier alnifolia*) and alder (*Alnus tenuifolia*); shrub meadows, which may be either wet or dry, supporting 40% to 60% coverage of shrubs; upland grass, dominated by grasses such as *Phleum pratense* and *Agropyron* spp.; and sedge meadow, a wet community with sedges such as *Carex atherodes*, *C. rostrata* and the grass *Calamagrostis canadensis*. Habitat types have been described in detail by Cairns and Telfer (1980). The Beaver Hills vegetation was mapped by Rowe (1972) as part of the mixedwood section of the boreal forest.



## METHODS

### Field techniques

During the spring and summer of 1973 piles of ungulate feces were counted on 937, 10 $m^2$ circular plots systematically situated along transects located by a multiple random start technique within six subdivisions of the park (Cairns 1976, Cairns and Telfer 1980). Winter feces (those dropped between leaf fall in autumn 1972 and green-up in spring 1973) were identifiable by color, consistency and position on top of the litter layer. Cervid feces piles were counted if they possessed more than 30 pellets (Neff 1968) and if more than half the pellets were inside the plot boundaries. All plots were assigned to one of the above-described habitats. Feces counts represent an index of time spent in the various physiognomic categories of vegetation. As such they may relate more to ungulate shelter requirements than to feeding.

Samples of feces were collected throughout the park from at least 30 winter defecations of each animal species along with samples of all potential food plants. Slides of fecal material were prepared for microscopic comparison with reference slides of known plant material as described by Sparks and Malechek (1968) and by Hansen (1971). Percentages of plant groups in composite samples of the feces were estimated by the inspection of 25 systematically located points on each of 20 slides representing each animal species. The fragment nearest the centre of the microscope field of each point was examined under 100X magnification and assigned whenever possible to a plant species or species group. Observations were considered to be reliable at the level of browse, forb, and graminoid categories. Less reliance was placed on identification to species but, since all identifications were done by the same individual, categorizations were considered consistant.

During most winters Parks Canada conducted aerial surveys of the entire park area. Location of observations of groups or individual cervids were plotted on 1:50,000 topographic maps. Surveys recorded bison as well during 1974 and 1976. (Bison have not usually been included in the aerial surveys because they were counted at the annual round up.) Counts were conducted from fixed-wing aircraft flying at 60 to 120 m above ground using experienced observers. Counts of moose, wapiti and bison are believed to be quite complete due to the deciduous vegetation and low terrain relief. Deer numbers and distributions may have been somewhat underestimated.

Ungulate distributions for the severe late winter of 1973-74, when snow depths in the region approached record levels, were compared with those for late winter 1975-76 when there was only a thin snow cover and temperatures had been mild. Based on examination of weather records from the Edmonton Industrial Airport those two winters are among the extremes for the last two decades. We selected 1973-74 and 1975-76 in preference to more recent data because there is evidence (Ferguson and Keith 1982) that the greatly increased numbers of nordic skiers since the late 1970s may have affected winter distribution patterns of ungulates.

Ungulate observations were recorded from the field survey maps by land survey quarter section (64.75 ha) blocks. Animals sharing quarter sections were assumed to be close enough for interaction as the size of moose home ranges in winter has been reported to be between 180 and 390 ha (Krefting 1974). For purposes of the present analysis, if individuals or



groups of moose were present by themselves in a quarter section they were not considered to be influenced by other species at that time. It is possible that quarter sections were used sequentially by various species, especially by wapiti and bison. Because most wapiti and free-roaming bison were restricted to the North Enclosure of the park, their distributional overlap with moose was calculated for that enclosure only. Distributional overlap measures for moose and deer were calculated using data for the entire park.

Data Analysis

Overlapping use of habitat, forage and space by moose with the three other ungulate species was evaluated by using the percent overlap index described by Anthony and Smith (1977). For example, if the deer diet were 8% (0.08) *Salix* and that of moose 23% (0.23) *Salix* then the overlap would be expressed as 0.08. Each species was considered to overlap the other with 0.08 of its own diet. The additional 0.15 of the moose diet consisting of *Salix* was not considered an overlap. Percentage overlaps were summed for all categories of each resource to estimate total overlap on that resource axis. Values for the total overlap could vary from 0 to 1.0.

Overlaps in winter habitat use and food habits were further analyzed by assigning arbitary index values to the various categories in each resource arranged in a continuum, then calculating mean indices for each ungulate species. (Food habits were placed on a continuum in taxonomic order while habitats were ranked in successional sequence.)

This made it possible to plot graphs of ungulate distribution along resource axes as Gausian curves (MacArthur 1972, May 1973).

Ungulate spatial distribution was quantified by a slightly different method. The mean number of animals of each species per quarter section in the North Enclosure was subtracted from the number observed in quarters with above average counts. The difference between the two values was then raised to the exponential to increase separation between species along the continuum, thus weighting the index values which had been previously assigned to quarter sections according to their position in the land survey grid system.

Mean values for each species on the three continua provided points in 3-dimensional space the interrelationships of which can be calculated using a measure called the index of dissimilarity, dpq. The equation for which is:

$$dpq = \frac{1}{M} \quad (U_{Jp} - U_{Jq})^2$$

where:

d = dissimiliarity index

M = number of variables

$U_{Jp}$ = position of species "p" on resource axis "J"

$U_{Jq}$ = position of species "q" on resource axis "J".

Further study of overlapping use of space employed Hurlbert's (1978) index no. 11. Values of Hurlbert's index close to 1.0 indicate that two species are both using a resource in proportion to its abundance. Values less than 1.0 indicate less overlapping use than expected by chance while values greater than 1.0 show overlapping use at a higher level than expected.



**RESULTS**

Data from analysis of fecal material collected after the winter of 1972-73 show that bison were strongly separated from cervids, especially moose, along the resource axis of food habits (Table 1). The 1972-73 winter was of average severity. The diet of bison was 99% herbage compared to 35.6% for wapiti, 43.1% for deer and only 2.7% for moose. Beaked hazel was the most important food catagory for moose with 31.5% of the diet and was nearly as important for deer at 25.0%. However, wapiti ate only 1.2%. Willows formed the largest group in the wapiti diet at 43.6% and were also important for moose at 22.6%, but formed only 7.8% of the diet of deer. The category of food items represented by fragments of saskatoon and trembling aspen was equally used by all three cervids, 18.4% in the wapiti diet, 18.1% in that of deer and 16.4% in the moose diet. Moose were, however, much greater users of white birch browse (17.1%) than were deer (2.6%) or wapiti (no recorded use). Moose in winter selected a diet with over 30% more browse than did other cervids. The difference was largely white birch, balsam poplar, buffaloberry (Shepherdia canadensis) and heavier use of beaked hazel.

Aerial surveys of moose showed a wide variation in numbers over the 15 years from which surveys were drawn (Fig. 1). The years between 1960 and 1968 saw a dramatic increase in total moose counts from 132 animals to 729. At that point, serious winter mortality was occurring and Parks Canada initiated a series of herd reduction slaughters which held total numbers in the 200-400 range for the rest of the period. Other parameters such as number of moose groups, number of quarter sections occupied by

Table 1. Percentage composition of identifiable fragments from ungulate winter diets in Elk Island National Park, based on microscopic analysis of feces from winter 1972-73.

| Plant Taxon | Wapiti | Deer | Moose | Bison |
|---|---|---|---|---|
| *Agropyron* spp. | - | - | - | 0.5 |
| Other grasses | 12.9 | 11.2 | - | 16.5 |
| Sedges (*Carex* spp.) | 22.7 | 31.9 | 2.7 | 82.0 |
| Total Herbage | 35.6 | 43.1 | 2.7 | 99.0 |
| Balsam Poplar (*Populus balsamifera*) | 0.6 | - | 5.5 | - |
| Willows (*Salix* spp.) | 43.6 | 7.8 | 22.6 | 1.0 |
| Alder (*Alnus* spp.) | - | 1.7 | - | - |
| White Birch (*Betula papyrifera*) | - | 2.6 | 17.1 | - |
| Beaked Hazel (*Corylus cornuta*) | 1.2 | 25.0 | 31.5 | - |
| Saskatoon and Trembling Aspen[1] (*Amelanchier alnifolia* and *Populus tremuloides*) | 18.4 | 18.1 | 16.4 | - |
| Buffaloberry (*Shepherdia canadensis*) | 0.6 | - | 4.1 | - |
| Highbush Cranberry (*Viburnum edule*) | - | 1.7 | - | - |
| Total browse | 64.4 | 56.9 | 97.2 | 1.0 |

[1]Reference slides of these two species proved very difficult to distinguish so similar fragments in the fecal samples were put into one category.



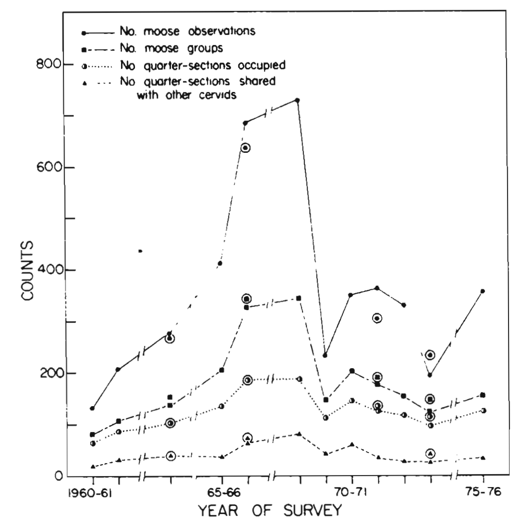


Figure 1. Numbers of moose and moose groups observed, number of land survey quarter sections occupied by moose and number of quarter sections shared by moose with other cervids in 16 winter aerial surveys of Elk Island National Park, Alberta, between 1960-61 and 1975-76. Circled values represent data from second surveys during the same winter.

moose and number of quarter sections shared by moose with deer and wapiti tracked changes in total moose numbers.

The initial comparison of resource use by moose with that of other ungulates showed a high level of overlap in winter habitat use, a substantial overlap in food habits with deer and wapiti but low overlap in food habits with bison and low spatial overlap in both mild and severe winters (Table 2). Overall, the greatest separation between the species was in the use of space.

Moose were placed in relation to other ungulates by the index of dissimilarity (Fig. 2). Moose were closest to deer in their resource use patterns and farthest from bison while intermediate with wapiti.

Use of the resource of space as defined by overlapping use of land survey quarter sections by moose with deer and wapiti showed that moose were significantly separate from both the other cervids (Fig. 3). On the other hand, moose exhibited a significant degree of togetherness by overlapping with each other more than expected by chance.

Values for spatial overlap shown in Table 2 and Figure 2 were for moose population levels as they were in the winters of 1973-74 and 1975-76. The impact of different levels of moose numbers on spatial overlap was evaluated for the relation of moose with deer and wapiti, the two other species counted in all aerial surveys. Overlap was found to be linearly related to moose population density (Fig. 4). A comparison was made of the total number of quarter sections occupied by moose at different population levels of moose (Fig. 5). The analysis showed that the dispersion of moose into additional range units is not quite linearly related to density. Rather, the curve flattens slightly as moose numbers



Table 2. Indices of overlap for four ungulate species in Elk Island National Park, Alberta[1].

| Resource dimension | Wapiti with moose | Deer with moose | Bison with moose | Mean |
|---|---|---|---|---|
| Winter food habits (F)[2] | 0.44 | 0.55 | 0.04 | 0.34 |
| Winter habitat use (H)[2] | 0.81 | 0.71 | 0.64 | 0.72 |
| Spatial distribution | | | | |
| Severe winter (S)[3] | 0.14 | 0.07 | 0.15 | 0.12 |
| Mild winter (S)[4] | 0.16 | 0.06 | 0.02 | 0.08 |
| Mean Indices (S + H + F) ÷ 3 | | | | |
| Severe winter | 0.46 | 0.44 | 0.28 | 0.39 |
| Mild winter | 0.47 | 0.44 | 0.23 | 0.38 |

[1]Calculated by method of Anthony and Smith (1977).
[2]1972-73 (data from Cairns and Telfer 1980).
[3]Mean of aerial surveys of 5-7 March and 15 March 1974.
[4]Survey of 5 March 1976.

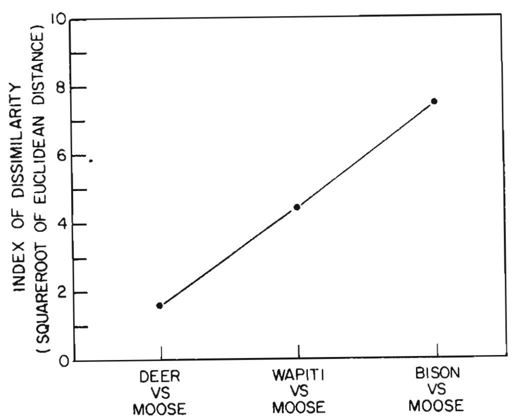


Figure 2. Index of dissimilarity between moose and other ungulates for three niche dimensions: food, cover during an average winter (1972-73) and spatial distribution during a severe winter (1973-74), at Elk Island National Park, Alberta.



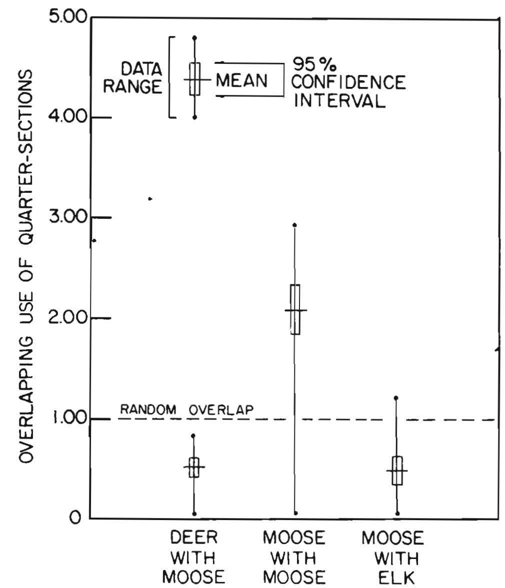


Figure 3. Means, 95% confidence intervals and data range for overlapping use of land survey quarter sections by moose with other moose and with deer and wapiti, calculated by applying Hurlbert's (1978) Index Number 11 to aerial survey data collected in Elk Island National Park, Alberta, from 1960 to 1976.

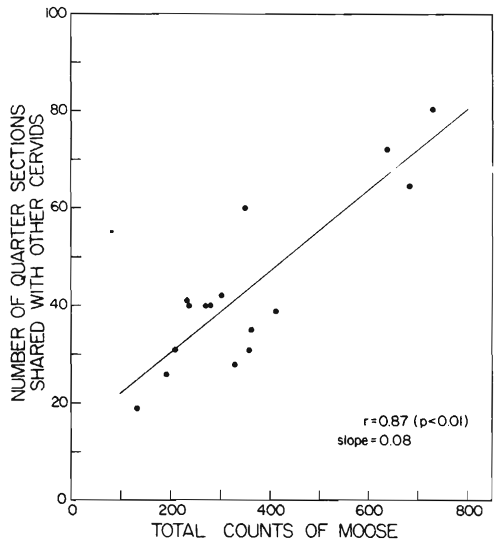


Figure 4. Number of land survey quarter sections shared by moose with other cervids in relation to the total counts of moose. Data from aerial surveys of Elk Island National Park, Alberta, from 1960 to 1976.



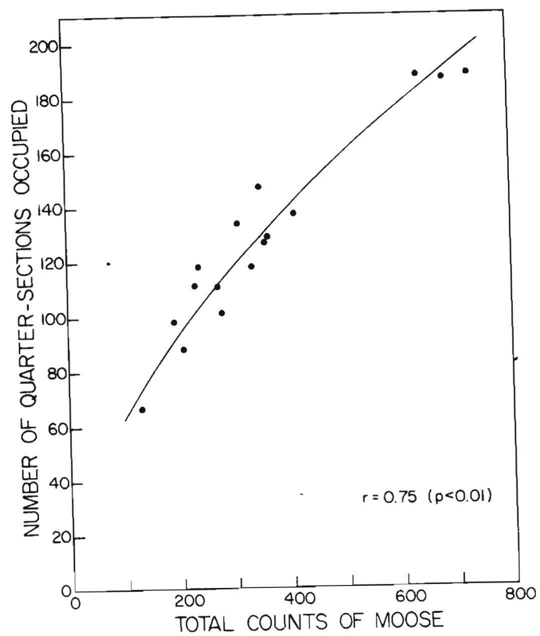


Figure 5. Relationship of total number of land survey quarter sections occupied by moose to total counts of moose. Data from aerial surveys of Elk Island National Park, Alberta, from 1960 to 1976.

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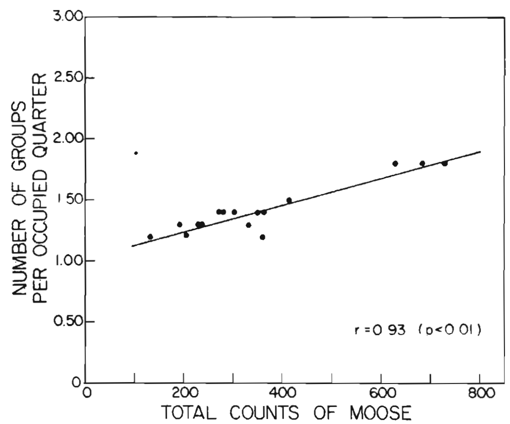


Figure 6. Mean number of groups of moose per occupied land survey quarter section in relation to total counts of moose. Data from aerial surveys of Elk Island National Park, Alberta, from 1960 to 1976.

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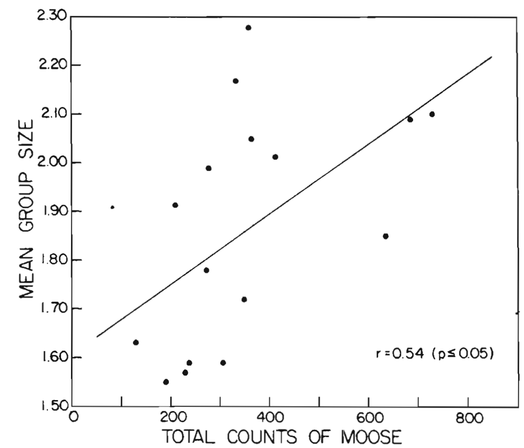


Figure 7. Mean number of moose per group as related to total counts of moose. Data from aerial surveys of Elk Island National Park, Alberta, from 1960 to 1976.

increase. This leveling-off is compensated for by an increase in number of moose groups per quarter occupied (Fig. 6) and an increase in the mean number of moose per group (Fig. 7).

## DISCUSSION

The flat topography and rather simple structure of the vegetation of the aspen parkland provides a limited variety of possibilities for niche separation among large mobile herbivores. Moose are at one end of the food continuum, feeding largely on twigs and leaves of woody plants (Peek 1974) while bison are at the opposite end, consuming little else than sedges and grasses. However, both deer and wapiti will eat a wide variety of plant parts and species, shifting from grasses, sedges and leaves to woody twigs in winter. The difference in food habits of moose and bison separate them sufficiently so that a substantial population of both should be able to exist in an area with interspersed meadows and shrubby vegetation. They have, in fact, done so for three-quarters of a century in Elk Island National Park (C. Blyth, unpublished data).

Overlap in use of vegetative types was much greater than that in food habits (Table 2). The mosaic interspersion of habitats at Elk Island put stands of all types within the cruising radius of all ungulates in the park, even in winter. Thus there was little possibility of partitioning the resource of sedge meadows, upland grass, shrubland and aspen forest although each species concentrated its activities in different types. Even bison overlapped extensively with moose through their use of aspen forest for bedding.



Overlap in use of land survey quarter sections was dramatically less than that for food and habitat (Table 2). Two trends in quarter section use can be discerned. On the one hand moose tended to be with other moose on the same quarters to a significant degree while being significantly apart from other cervids (Fig. 3). On the other hand the occupation of new quarter sections by moose as density increased was nearly proportional to population growth until a substantial proportion of the quarters available were occupied (Fig. 5). For instance, a population of 200 moose would be expected to occupy 94 quarters and 400 moose, 140 quarters. Even more striking was the linear relationship of quarter sections shared with other species to moose numbers. At a level of 200 moose, 30 quarters would be expected to be shared while 400 moose would be expected to share 47 quarters (Fig. 4). This increase was also somewhat less than proportional. However, when number of shared quarter sections was plotted against total number of quarters occupied by moose it was apparent that a doubling of the number of occupied quarters produced slightly more than double the overlap (Fig. 8). The significant togetherness of moose (Fig. 3) probably results from the association of cows with their calves of the previous summer. Of 5267 moose counted in 2752 groups 84% were in groups of three of fewer animals (Cairns 1976).

The lack of proportional increase in distribution and overlap as population increased probably reflected an aversion to the close proximity of deer and wapiti as well as slightly different habitat preferences. Although the major habitat types occurred to some extent on all quarter sections, their proportions and interspersion varied considerably.

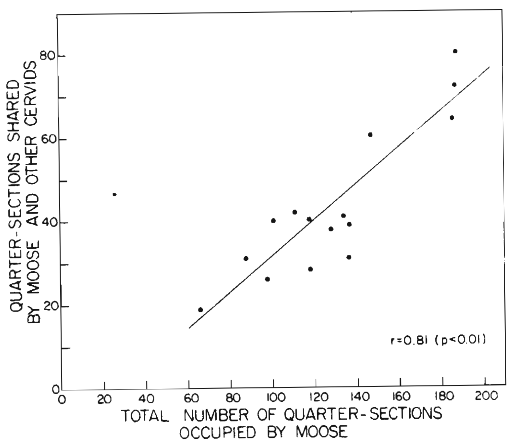


Figure 8. Numbers of land survey quarter sections shared by moose with other cervids in relation to the total number of quarter sections occupied by moose. Data from aerial surveys of Elk Island National Park, from 1960 to 1976.



Disturbance by humans probably had some effect on moose distribution as was established by Ferguson and Keith (1982) for nordic skiing activities. Wapiti have been observed to be behaviorly dominant to moose. Cow/calf groups of wapiti that encounter a moose, often indulge in a form of "mobbing" behavior, walking up close to the moose and staring at it until the moose becomes agitated and moves off (R. Hudson, personal communication). It is also probable that previous heavy use of quarter sections, especially by wapiti, may render them less desireable to moose because of removal of much of the previous year's browse yield. Since there was no renewal of food supply during the winter, a quarter heavily browsed by a large group of wapiti early in the season might be avoided by moose all winter. Such behavior has been reported from Riding Mountain National Park by Rounds (1981).

In spite of the strong relationship between proportion of the Park occupied by moose and population increase over a certain range of area proportions, the impact of the presence of other ungulates on moose behavior was apparent. It was noteworthy that although most quarter sections contained similiar habitat, moose were never observed on more than 67% of them on any single aerial survey (Fig. 5). Densities of moose were then over 3/km$^2$, a very high level compared to other populations (Telfer 1984) and pressure to disperse must have been extreme. Packing of moose on occupied quarters in the form of larger group sizes and more groups per quarter also occurred as the population increased (Figs. 6 and 7). Those trends suggested that moose were to some degree avoiding areas well populated by other ungulates. It thus appears that resource partitioning between moose and other cervids in the Elk Island enclosures was largely a function of dispersal behavior and seasonal movement, facilitated by the quite general food habits and habitat requirements of the species involved.

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