

MODELLING A HUNTED MOOSE POPULATION IN NEW BRUNSWICK

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ABSTRACT: To explore the role of hunting in population dynamics, a deterministic simulation model was built to mimic a real moose (*Alces alces*) population in a 2396 km² area of southeastern New Brunswick. Data from moose population statistics in southeastern New Brunswick were used to initialize the model's variables. Harvest rates above 6%, if no antlered males were shot, and 9.5%, if only antlered males were shot, initiated a decrease in the population. Maximum sustained yield was estimated in the model to occur at 0.4 moose per km². Hunting was an additive mortality factor at densities below 0.4 moose per km². Hunting after the rutting period allowed a harvest rate 10% higher than before or during the rut. At harvest rates less than 5%, time of harvest relative to the rut was inconsequential. There was little benefit in distorting harvest sex ratio above 60% antlered males. Although hunting was an important mortality factor, moose populations in southeastern New Brunswick appeared ultimately to be driven by natural mortality factors and poaching of the adult cohort. The potential role of hunting in population dynamics is limited by the magnitude and timing of non-hunting mortality factors.

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Hunting in any form reduces a population from its ecological carrying capacity (equilibrium between animal numbers and food/habitat availability) to a new equilibrium at a lower density of animals and a higher density of food/habitat (Caughley 1979). Legal hunting is the mortality factor over which man can most easily exert control; hence, it becomes a focal point for study in population dynamics. The effect of hunting on population dynamics is likely variable. Anderson and Burnham (1976) concluded that hunting loss for mallards (*Anas platyrhynchos*) below a certain level was compensated by changes in other mortality factors and that additivity occurred only above a threshold level. Knowledge of the conditions under which hunting is additive to or compensatory with other mortality factors and what population parameters characterize the transition are crucial to sound decisions on harvest management.

Time and social consequences often make it impractical to manipulate a real population to explore the full range of population responses to hunting. Modelling allows such

experimentation without putting a real population at risk. A model can be used as a simulator of ecological processes, although it is necessarily a simplified caricature of the real world. In defining a relationship between hunting and population dynamics we must capture the essential processes controlling population size and impose various harvesting strategies in a manner that realistically impinges on these processes.

The present paper utilizes a model to mimic a moose (*Alces alces*) population in southeastern New Brunswick. The thrust of the present modelling exercise is to understand the impact of exploitation through hunting. Understanding leads to the predictive ability necessary in adaptive management (Holling 1978).

METHODS

The Model

The deterministic model simulated a moose population through an annual cycle of births and survivorship for 25 years (Fig. 1). Statistics from moose in southeastern New Brunswick were used to initialize density,

age and sex composition, productivity, and carrying capacity in the model. Although the form of relationships linking reproductive performance and mortality to carrying capacity, sex ratio, range quality, and winter severity are known qualitatively, they are not well quantified in the literature. Hence, values were estimated from available literature and from judgement. Accuracy of the predictions from this model necessarily depends on the accuracy of model inputs and the level of biological realism captured in the algorithms. Moen and Ausenda (1987) cautioned that critical population parameters can have a multiplicative effect on growth of modelled populations. Hence, small errors in parameter values can produce, with time, an increasing difference between the paper population and the real one.

The 2396 km² study area was centered 120 km east of Fredericton, N.B. This area has a fire history and ongoing logging operations, as do most of the forests in moose range. Habitat quality is expected to change through time and space as a result of forest development. Habitat conditions for moose, then, are not uniform throughout an area and locally reflect unique influences of soil, topography, and disturbance history. The model assumes that carrying capacity is constant over the entire area, although habitat quality varies kaleidoscopically within the area over the 25-year time frame. Specifically, all habitats are assumed to be equally accessible to moose anywhere on the area. The model assumes that the mosaic nature of the forest and habitat use by moose are such that the net influence of habitat on the population remains constant over a 25-year period; specifically, natality and mortality factors are not influenced by spatial variability in habitat quality. The assumption of constant net effects of habitat is probably reasonable in light of the large home range and movement of moose: 10 - 20 km² home ranges (Van Ballenberghe and

Peek 1971, Phillips *et al.* 1973, LeResche 1974, Roussel *et al.* 1975, Lynch 1976) and seasonal movements of 32 km (Houston 1968, Goddard 1970). Moose are not territorial, spacing themselves instead with an individual distance (Geist 1963), and home ranges overlap. Moose population response over an entire area is a summation of relationships between individuals and resources within their respective home ranges.

Initialization of Variables

Density dependence is a major component in population dynamics (Keith 1974, Caughley 1977). Conceptually, the relationships between survival, production and ungulate density acting through food limitation has been well reviewed (Watt 1968, Caughley 1979, McCullough 1979). Ungulate populations manifest a response to rising density and shrinking resources before ecological carrying capacity (K) is reached (McCullough 1979). The density at which populations begin to slow in growth is usually approximately 0.67 K (Caughley 1979, McCullough 1979).

An ecological carrying capacity of 0.6 moose per km² was calculated from data between 1937 and 1963 in Fundy National Park, approximately 75 km south of the present study site (Kelsall 1963); 0.6 moose per km² was used as K in this study. In each iteration, the model calculated a new moose density and compared it to the K value of 0.6 set in the initialization phase. The percentage difference was stored in an array holding a moving 4-year history. In this way a variable called NK, a "short term" carrying capacity, was calculated (Fig. 1) that was intended to reflect the influence of present and past numbers of moose on resources for future moose. The most recent difference value added to the array contributed 40% to NK, decreasing 10% annually over the next 3 years, before the value was deleted. For example, densities above K in one year will reduce NK and the

START OF SIMULATED YEAR (1 JANUARY)

POPULATION AT BEGINNING OF WINTER

Males: Adults, Yearlings, Calves
 Females: Adults, Yearlings, Calves

CALCULATE DENSITY (d), COMPARE TO ECOLOGICAL CARRYING CAPACITY (K) AND CALCULATE SHORT-TERM K (NK)

$$NK = 0.4 \frac{(K-d_t)}{K} + 0.3 \frac{(K-d_{t-1})}{K} + 0.2 \frac{(K-d_{t-2})}{K} + 0.1 \frac{(K-d_{t-3})}{K}$$

WINTER MORTALITY

1. Reduce calves 5%, yearlings 2%, adults 5%
2. Multiply survivors by DENFAC (Figure 3)

CALCULATE SPRING POPULATION

ADVANCE AGES OF SURVIVORS

1. At female densities (B) $< 0.67 NK$, calf production set at 100 calves: 100 adult females and 40 calves: 100 yearling females;
2. At female densities (B) $\geq 0.67 NK$, calf production is calculated from Figure 4;
3. Reduce calf production when % males among adults in previous autumn is < 40 (Figure 5).

REMOVE CALF MORTALITY (SUMMER)

1. Calculate calf mortality rate as function of female density in winter (Figure 7) and remove calves.
2. Remove 4% of calves (predation).
3. Remove 11% of calves (accidental and unknown losses).

REMOVE ADULT AND YEARLING MORTALITY (SUMMER)

Set at 5% of age and sex classes

REMOVE POACHING LOSSES (LATE SUMMER)

Set at 1% of all age and sex classes

REMOVE MOOSE TAKEN BY HUNTING

Specify harvest rate for age and sex cohorts.

CALCULATE SURVIVING ADULT MALES: FEMALES AND BREED FEMALES

REMOVE MOOSE LOST TO POACHING

Set at 5% of all age and sex classes

CALCULATE POPULATION AT BEGINNING OF WINTER

Males: Adults, Yearlings, Calves
 Females: Adults, Yearlings, Calves

RETURN TO START FOR NEXT SIMULATION YEAR

Figure 1. Sequence of calculations in a simulated year in moose model. Position of hunting removal relative to breeding season is variable in model.

effect will decrease over the next 3 years. Damaged range was assumed to fully recover in 5 years if moose densities were held below K . NK cannot exceed K . In each iteration, all calculations involving density dependence employed the current NK value.

Aerial surveys in the study area in February 1984 and 1985 were used to determine the number of moose in the starting population on 1 January of year zero. An observation efficiency rate of 0.7 (LeResche and Rausch 1974, Crête *et al.* 1985) was used to correct for missed animals. Animals were classified as adult males, adult females, or calves. The proportion of yearlings among adults in winter was estimated from harvest data (Boer 1987). Calves were assumed to exhibit a 50:50 sex ratio.

Sensitivity Analysis

Since there is not equal confidence in all the estimates of relationships in a model, sensitivity analysis was performed to discover where error would be most damaging to the forecasts. Sensitivity analysis was conducted by incrementally changing a variable while holding others constant and evaluating the effect of error on the forecast outcome. Sensitivity in model response is measured as the deviation of output measures from those of the standard run. If a small change (error) in a variable results in a large change in model outcome then outcome is sensitive to uncertainty in that variable.

Winter Survival

Southeastern New Brunswick has comparatively mild winters. Thus, winter survival rate of calves was set to 0.95 in the model. This rate was chosen because, although none of the 11 radio-collared calves from a field study (Boer 1988a) died during winter, undoubtedly some do perish. A 0.95 winter survival rate brings total annual calf survival in line with the 0.68 survival rate

calculated by Boer (1988b). In the more rigorous winter environment of northwestern Alberta, Hauge and Keith (1981) calculated a survival rate of 0.81 for calves (Jan-Apr); most mortality was from wolves (*Canis lupus*), which do not occur in New Brunswick. A winter severity index was calculated from an additive relationship between snow depths and ambient temperatures (Jenkins 1987). If the index exceeded an arbitrary threshold of 20, calf survival decreased exponentially (Fig. 2). Calves of both sexes were treated similarly. Winter severity indices for the 25-year simulation period were set in the model at initialization. Simulations reported here were done with the winter severity index set below the threshold, although the model was designed for use in areas with severity indices above threshold.

Survival rates of 0.95 and 0.98 were used for adult and yearling moose, respectively, regardless of the winter severity index. These rates were estimated from a partitioning of annual survival rates calculated in Boer (1988b). Death during winter is probably more a consequence of factors such as accidents, old age, and winter tick (*Demacentor albipictus*) infestations, confounded by the additional stress of even a mild winter, than of malnutrition. Resources available to moose determine their winter survival rates; in Kenai, Alaska, winter survival was much higher on "good quality" than on "poor" range (Bishop and Rausch 1974). To simulate the influence of a diminishing share of resources on winter survival as density rises, survival in all cohorts decreased as density exceeded 0.67 NK (Fig. 3). Conceptually, the relationship of decreasing winter survival with increasing density is sound but the threshold and slope of the line are speculative.

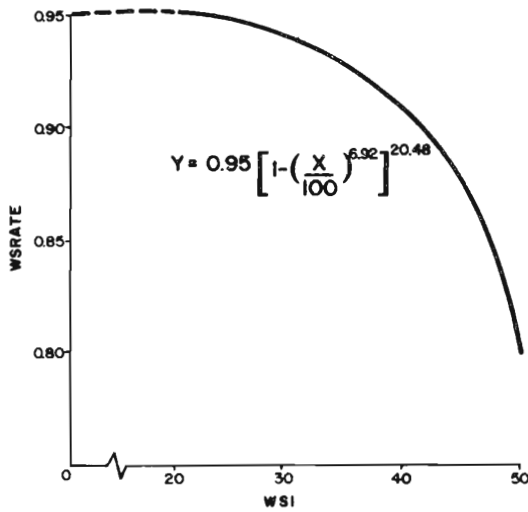


Figure 2. Speculated relationship between winter survival rate (WSRATE) of moose calves and winter severity index (WSI). Severity indices are composed of average snow depths and temperatures over the winter period. Winters in southeastern New Brunswick have indices ≤ 20 (A.H. Boer, unpubl. data). An index value of 50 was set as the most severe possible for New Brunswick.

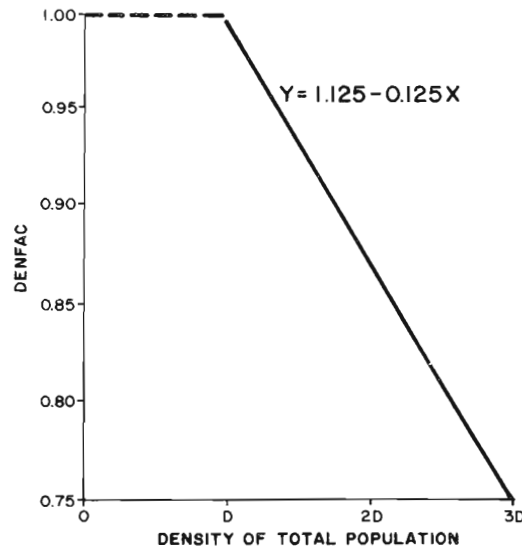


Figure 3. Speculated relationship between total population density (moose/km²) and density factor (DENFAC, a multiplicative descriptor of winter survival). The value of D is equivalent to 0.67 of carrying capacity (NK) in the simulation model; as population density increases above D, winter survival decreases.

Calf Production

Maximum production was set at 100 calves (50:50 sex ratio) per 100 adult females and 40 calves per 100 yearling females (Boer 1987). As density of adult and yearling females in winter increased above 0.67 K the rate of calves born decreased (Fig. 4). These density response curves mimicked studies reported by Blood (1974) and Markgren (1982). Female density (adults and yearlings combined) alone was used since breeding females with calves select different habitat than other moose (Peek 1971, Peterson 1977, Thompson and Vukelich 1981); we speculate that female-female interactions are most important. Clutton-Brock *et al.* (1982) and Gavin *et al.* (1984) concluded that female breeding success in red deer (*Cervus elaphus*) and white-tailed deer, (*Odocoileus virginianus leucurus*), respectively, was dependent primarily on

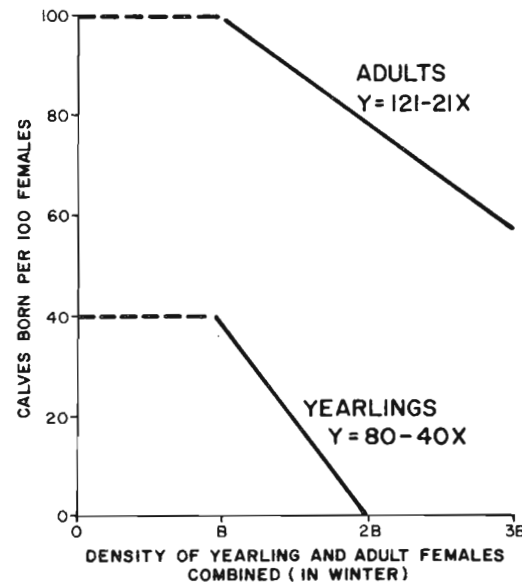


Figure 4. Production curves of females with varying winter density of yearling and adult females (DENFEM) in moose population simulation model. B is set at 0.67 of carrying capacity (NK) and $X = \text{DENFEM}/B$.

quality of female home range and social rank among females.

Sex ratio of adults was speculated to be important to fertilization rates and, hence, production of calves (Bishop and Rausch 1974). A minimum of 40 bulls (≥ 1.5 years old) were believed necessary to breed 60 adult females in Quebec (Crête *et al.* 1981); densities there were slightly higher than in this study. Because moose in the northeast do not form harems, this high ratio (0.4:0.6) seems reasonable in a densely forested region with a density of moose as low as in New Brunswick. In the model, number of calves born per 100 adult or yearling females was multiplied by a birth rate multiplier, ≤ 1.0 , depending on the ratio of adult males to adult females the previous autumn. If adult sex ratio decreased below 0.4 males:0.6 females, the birth rate multiplier decreased at an increasing rate (Fig. 5).

The influence of winter on productivity in southeastern New Brunswick was considered minimal. To improve the versatility of the model in areas with more severe winter, the option of simulating an influence of winter on productivity was built-in (Fig. 6).

Summer Mortality

Annual calf mortality in the study area was estimated at 20-30% (Boer 1988a); most of that mortality is expected early in life (Ballard *et al.* 1981). In the model, calves are removed during summer in 3 steps, each attributable to different factors. First, quality of calves and, hence, their survivability, is presumed to be dependent on resources available to their mothers during pregnancy, as for red deer (Clutton-Brock *et al.* 1982). Therefore, density of females in winter relative to carrying capacity was explicitly accounted for. At the current female density, $0.1/\text{km}^2$, neonate mortality is estimated at approximately 0.03 (Fig. 7). The slope of the line linking density and mortality rate of neonates is speculative. Black bears (*Ursus*

americanus) prey on neonate moose in New Brunswick but few are taken (Boer 1987). A fixed mortality rate of 0.04 was used to simulate these losses. Surviving calves were then further reduced at a fixed rate of 0.11 to mimic summer losses from density-independent accidental and unknown causes (Boer 1987).

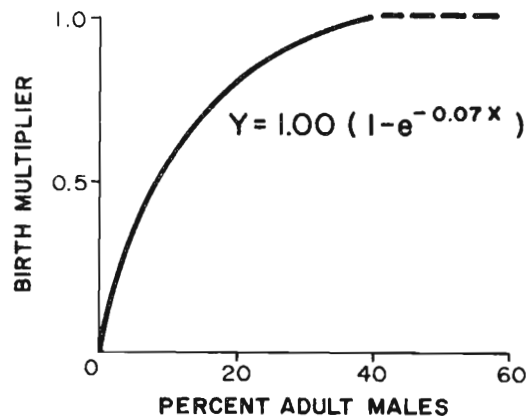


Figure 5. Estimated influence of adult sex composition on moose calf production. The potential number of calves born into the simulated moose population (Fig. 4) is multiplied by birth multiplier.

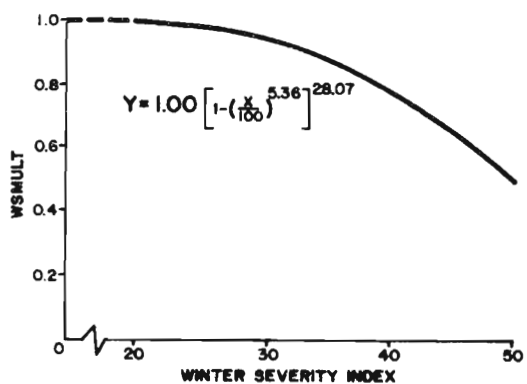


Figure 6. Estimated impact of winter on calf production. The winter severity multiplier (WSMULT) represents the percentage of potential calf production (product of Figs. 4 and 5) that will actually be born into the simulated moose population.

Mortality of adult moose occurs in summer in New Brunswick from accidents, including roadway collisions with vehicles and from *Parelaphostrongylus tenuis* (Smith *et al.* 1964), but the magnitude is unknown. Since the moose population on the study area was stable (Boer 1987), summer mortality rate was calculated as the rate that stabilized a simulated population incorporating size, structure, productivity, hunting loss, and other mortality rates estimated for the real moose population on the study area. An arbitrary mortality rate of 0.05 was set as a base level for yearling and adult moose, chosen because it stabilized the simulation population and hence mimicked the moose population on the study area.

Poaching Loss

Poaching can be an important mortality factor of moose (Vilkitis 1971) and is common in southeast New Brunswick. Because poaching rates can be modified by enforcement strategies, the model accounts for poaching loss explicitly.

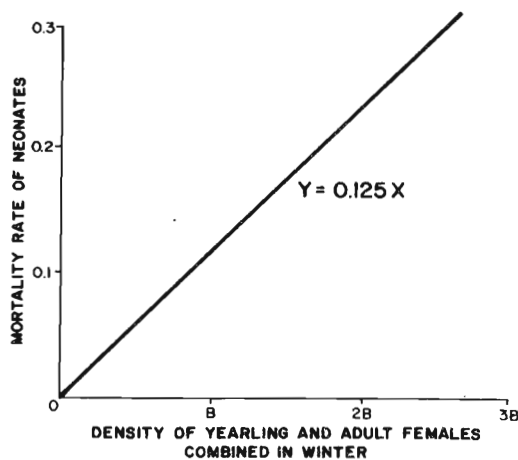


Figure 7. Estimated relationship between density of yearling and adult females in winter (DENFEM) and mortality rate of calves during summer. B is set at 0.67 carrying capacity (NK) and X is defined as DENFEM/B.

Because of its nature, the real magnitude of illegal loss is not known. Enforcement staff with DNR in southeastern New Brunswick were interviewed about timing and extent of poaching activity. A consensus was that 5% of the standing population in autumn was lost to poaching over the ensuing 12 months. While some illegal hunting and snaring is expected every month, about 20% is believed to occur in late summer, before breeding, and the bulk, 80%, during the deer (*Odocoileus virginianus*) hunting season beginning in late October. Losses to poaching in other months are not explicitly accounted for, although they may be reflected in winter and summer mortality rates.

Hunting

Hunters can be effective predators and will concentrate their efforts in areas used by moose. Hunter access is augmented by forest roads constructed for the harvest and transport of wood or for control of forest fires. Because these disturbances also produce early successional stages and hence "good" moose habitat, hunting pressure is expected to be greatest in good moose areas.

Since present exploitation is heavily biased towards adult males (A.H. Boer unpubl. data), affecting adult sex ratio, the temporal juxtaposition of a hunting season and peak of breeding is important. Three options that vary the temporal positions of hunting and poaching losses with respect to breeding times were included in the model: hunting prior to the peak of breeding mimicking the current order of events in New Brunswick, hunting immediately after the breeding season, and hunting midway through the period of high poaching loss.

Harvest rate and composition are input variables and any combination of rate and target cohorts can be tested. Whatever the harvest rate, an additional 10% of the harvest was removed from the cohort as a wounding loss.

RESULTS AND DISCUSSION

Sensitivity Tests

For a standard run, all initial conditions and driving variables were set in the model to simulate the current moose population on the study area (Tables 1 and 2). The modelled population was harvested annually to simulate current rates and vulnerability factors (Boer 1987). The standard run projects the present population 25 years into the future under the assumption that present relationships continue (Table 3). The output was used as the standard against which simulations of management interventions and those quantifying sensitivity can be compared. The apparent stability in numbers mimics well the current trend in the moose population on the study area (Boer 1987).

Table 1. Initial conditions and driving variables used in standard run to simulate the moose population on a 2396 km² study area in south-eastern New Brunswick. Values reflect field estimates from the study population.

| Variable | Value |
|--|-------|
| Population 1 Jan - Year 0 | |
| Calf Males | 63 |
| Calf Females | 63 |
| Yearling Males | 36 |
| Yearling Females | 48 |
| Adult Males | 85 |
| Adult Females | 184 |
| Starting Density (moose/km ²) | 0.2 |
| Ecological Carrying Capacity (moose/km ²) (constant) | 0.6 |
| Winter Severity Index (constant) | 20 |
| Calf Production | |
| Calves/100 Ad F | 100 |
| Calves/100 Yrl F | 40 |
| Harvest Rates % (Table 2) | |
| Adult Males | 20 |
| Adult Females | 7 |

Table 2. Calculation of harvest rates for moose population on 2396 km² study area in south-eastern New Brunswick from Boer (1987).

| | Ad M ^a | Ad F ^a | Calves |
|--|-------------------|-------------------|--------|
| Legal harvest ^b | 35 | 19 | 7 |
| Wounding loss (0.10 x harvest) | 4 | 2 | 1 |
| Poaching loss (0.5 x harvest) | 18 | 10 | 3 |
| Estimated post-hunt population ^c | 121 | 232 | 126 |
| Autumn population before hunting | 178 | 263 | 137 |
| Harvest rate (%) ^d | 20 | 7 | 5 |

^a Yearlings are included as adults.

^b Check station data (average).

^c Aerial survey data from winter following hunt.

^d Harvest divided by autumn population.

Starting Sex Composition of Adults: - To test sensitivity to error in adult sex ratio, adult composition was varied from 25 to 50% male by steps of 5%, with yearling sex ratio held constant at 50:50. After 25 years, total population size decreased approximately 14%, and harvests decreased 13%, as percentage males increased from 25% to 50%. Simulation outcomes are not very sensitive to changes in adult sex composition of the starting population. The standard run used an adult composition of 32% males in the starting population.

Initial Age Composition - Because only a fraction of animals on the study area were observed during the winter aerial surveys the estimated age structure contains uncertainty. Beginning the simulation run with only adults (no calves or yearlings) produced a projected population in year 25, 17% greater than the standard run, which was made with 56% adults. Adults could constitute between 45% and 65% of the animals beginning a

Table 3. Model output from simulated moose population on a 2396 km² study area in southeastern New Brunswick. Variables used in the standard run are summarized in Table 1.

| Year | January Population | | | | | | |
|------|--------------------|--------|----------|--------|-------|--------|-------|
| | Calves | | Yearling | | Adult | | Total |
| | Male | Female | Male | Female | Male | Female | |
| 0 | 63 | 63 | 36 | 48 | 85 | 184 | 479 |
| 1 | 65 | 65 | 37 | 48 | 81 | 183 | 479 |
| 5 | 64 | 64 | 37 | 49 | 77 | 183 | 474 |
| 10 | 63 | 63 | 37 | 48 | 75 | 181 | 467 |
| 15 | 63 | 63 | 37 | 48 | 74 | 180 | 465 |
| 20 | 62 | 62 | 36 | 47 | 74 | 178 | 459 |
| 25 | 62 | 62 | 36 | 47 | 73 | 176 | 456 |

simulation sequence with little effect on outcome.

Predation Rates - Predation influences only calves, and the model is sensitive to changes in calf survival. Doubling predation losses from 4% to 8% triggered an 18% reduction in total population from the standard run in 1 January, year 25. Simulation results were sensitive to calf losses due to predation.

Calf Production Rates - Three combinations of production rates were tested. These were, changes in both yearling and adult rates, adult rate only, and yearling rate only. Because adult females are more numerous than yearlings and produce more calves per female, model response is most sensitive to changes in adult productivity. Changing yearling productivity by 33% while holding adult production constant (100 calves per 100 cows) resulted in only a 6% change in both total population and harvest. However, increasing both adult and yearling productivity 10%, increased total population 51% by year 25. Total population in year 25 was 39% less than standard when production of yearlings and adults was reduced by 10%. Hence,

model forecasts are sensitive to changes in productivity, particularly of adults.

Poaching Rates - A 20% increase in poaching rates decreased total population size at year 25 down 25% and projected harvest down 24%. Both harvest and population rose 32% by year 25 when poaching rates were reduced 20%. Population size and harvest diverged steadily from standard values with time.

Management Implications

Nomograms - Nomograms can be useful tools to scan a wide range of policies for evaluation in resource management (Peterman 1975, Larkin 1977, Holling 1978). Once a policy area has been selected the detailed model and year-by-year outputs can be used to evaluate specific policy options. Nomograms depicting response surfaces of 5 selected parameters to changing harvest rate and to the proportion of antlered males can be grouped together to facilitate comparison (Fig. 8). Each of the 5 parameters is measurable in the actual population and predictions can be tested. Nomograms can also be used to depict the temporal change for a

particular parameter (Fig. 9). By examining combinations of harvest rate (HR, % of total autumn population harvested) and proportion of antlered males (PAM) in harvest, decision makers can compare future consequences of a wide array of possible policy decisions over time.

Harvest rates greater than 6% if no antlered males are shot, and 9.5% if only antlered males are shot, result in a decrease in population (Fig. 8e, curve A). Maximum harvest rate when $r = 0$ occurred at 10% HR with 75% of the harvest composed of antlered males. At this point, total population on 1 January was 35% (500 animals) of ecological carrying capacity (K). Maximum harvest of 110 animals occurred at a 1 January population of 1,000 moose (0.7K), with HR set at 7% and PAM between 85-90% (Fig. 8a).

Time of Harvest - In the modelled population (Table 1), hunting after the rutting period allowed a HR 10% greater than when hunting occurred before the rut. Hunting late ensures the maximum number of females have been bred and harvests are less sensitive to changing proportions of males. Hence, hunting moose after the rutting period is a more robust harvest strategy than hunting during or before rut. At harvest rates less than 5%, time of harvest relative to the rut was inconsequential.

Calf Harvest Rates - Increasing the proportion of calves that are harvested from 5% to 20% (males ≥ 1.5 years old harvested at current rates, females ≥ 1.5 years old not harvested), the projected total population increased 85% and harvest increased 59% by year 25. Because adult females were not hunted in these tests, the additional calves produced, more than offset the increased calf mortality to hunting. By harvesting 30% of the calves, the projected population grew 2% and harvest 1% in 25 years. The ability of the

calf component to absorb hunting losses without initiating population declines is a function of the magnitude and timing of other mortality factors. High neonate predation losses, as reported in some Alaskan studies (Franzmann *et al.* 1980), reduces allowable calf harvests.

Additive - Compensatory Hunting Mortality - The nature of an additive - compensatory relationship depends on the degree of flexibility in factors affecting natural mortality. Compensation to hunting losses is possible only above densities at which density dependent effects begin to operate. There are 2 dimensions to the question of additive - compensatory hunting mortality: (1) threshold harvest rate and (2) threshold density relative to K. By definition, compensatory hunting mortality replaces some nonhunting mortality such that total annual mortality remains unchanged. Hunting is additive at densities below 0.7K (Table 4) because density dependence is not functioning. As the modelled population grows beyond 0.7K, density-dependent processes operate and these mechanisms control the population's trajectory as density approaches K. Partial compensation to hunting mortality occurs at densities above 0.7K since hunting mortality reduces population density, which in turn improves both juvenile and adult survival. Hunting can be additive in this region if harvest rate exceeds the capacity of the modelled processes to adjust natural mortality rates and productivity rates. Since hunting in the model is focused primarily on middle-aged moose (Boer 1987), the cohort with the lowest natural mortality rates, additivity should be expected at even low harvest rates. For the modelled population, as density increased above 0.7K, harvest of adult females became increasingly compensatory (Table 4). At K, harvest above 3% of adult females was additive.

Additive hunting mortality does not nec-

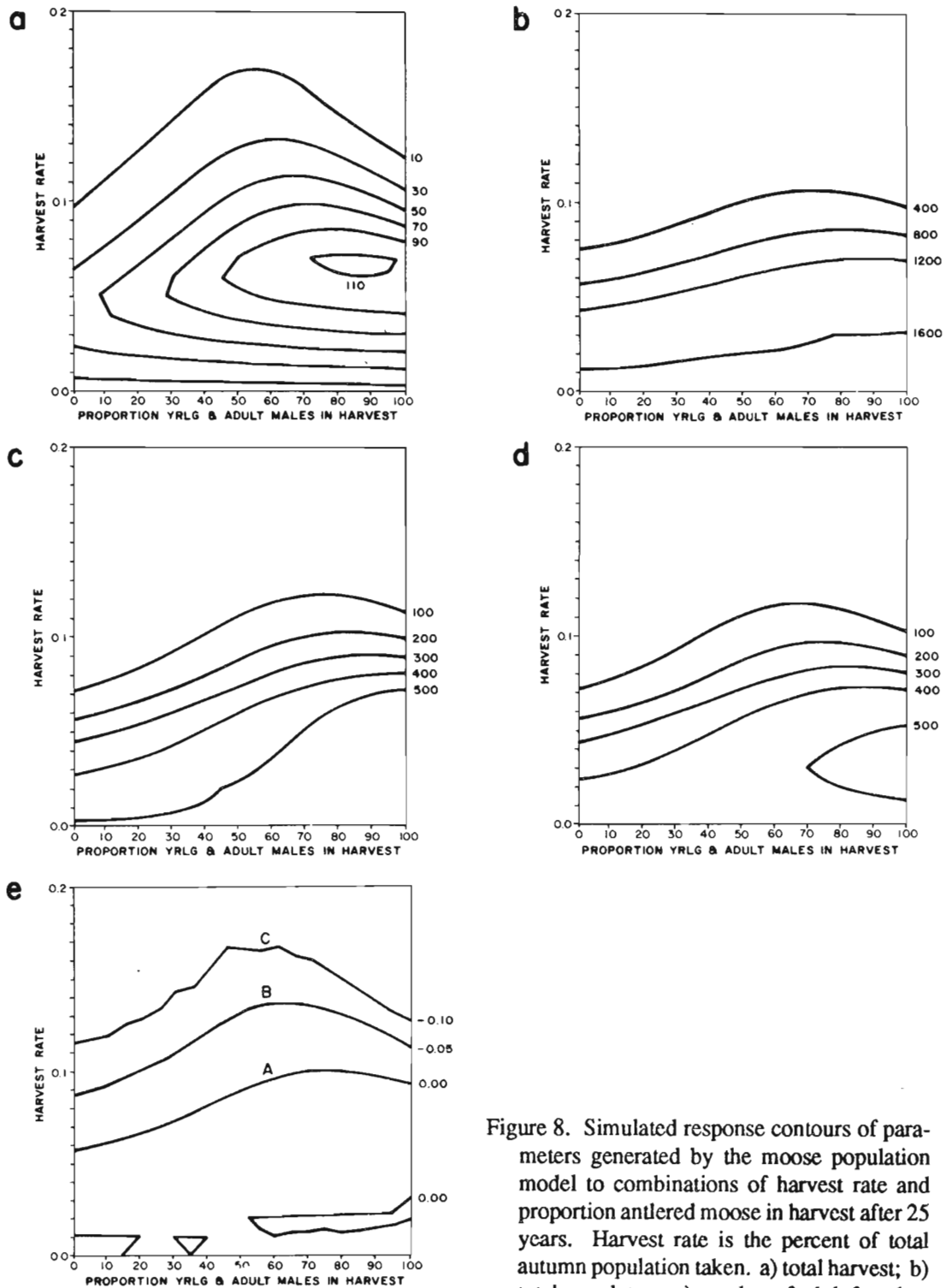


Figure 8. Simulated response contours of parameters generated by the moose population model to combinations of harvest rate and proportion antlered moose in harvest after 25 years. Harvest rate is the percent of total autumn population taken. a) total harvest; b) total population; c) number of adult females; d) calf production; e) rate of population change r .

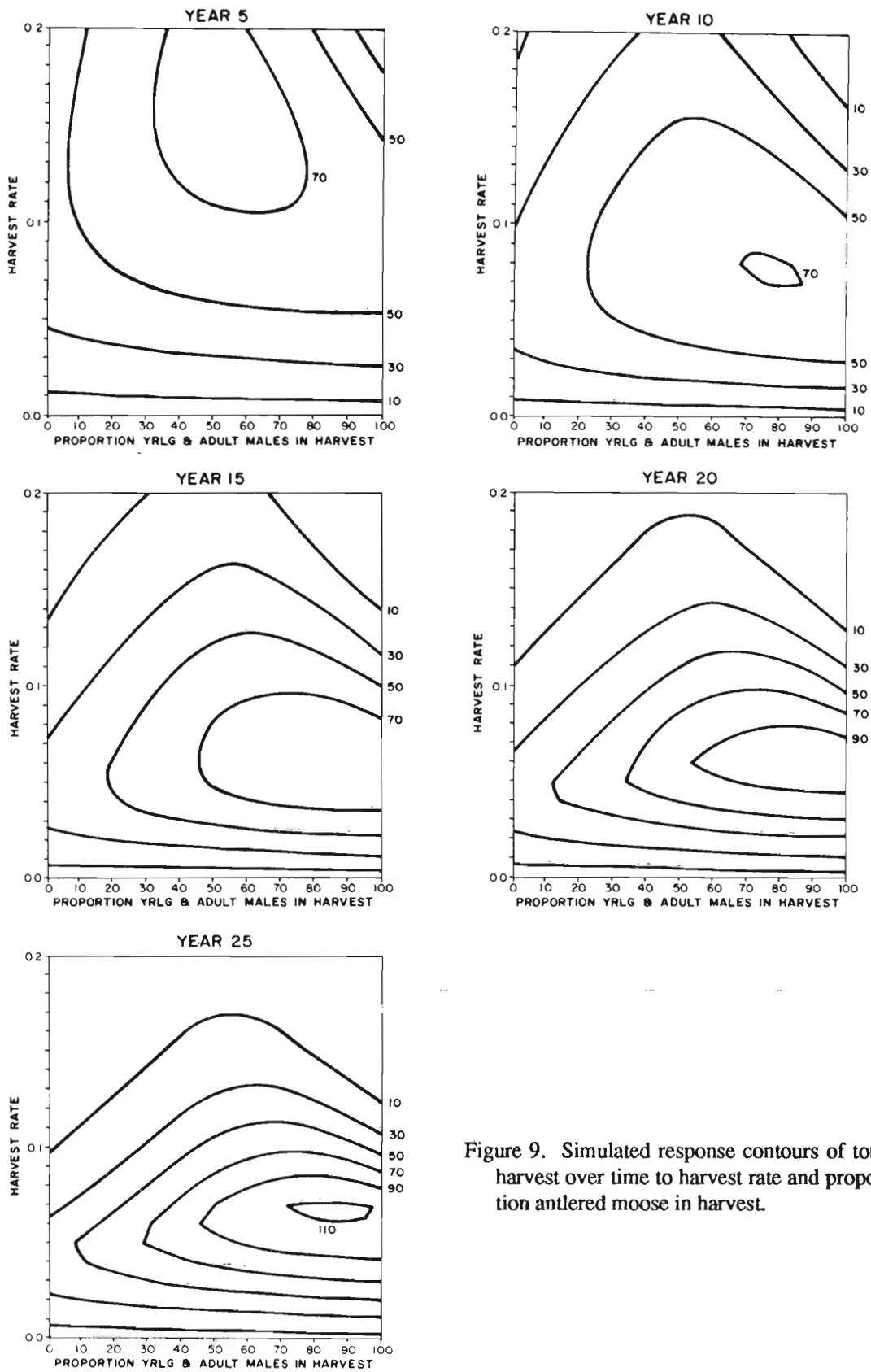


Figure 9. Simulated response contours of total harvest over time to harvest rate and proportion antlered moose in harvest.

essarily imply populations will decrease. The Lake Stream population has stabilized (1973-1985) at a density of 0.2 moose per km² (0.33K) with a harvest rate of 10% (Boer 1987); if the model abstraction is reasonable, then all of the hunting mortality is additive (Table 4). However, exploitation carries a risk of taking an excessive harvest. A moose population is dynamic and variability associated with winter weather, natural mortality factors, and hunter harvest is inherent. Determination of the allowable error (overharvesting) is of interest because game agencies find it difficult to completely regulate harvest and a wide confidence interval is usually associated with estimates of density, natural mortality factors, winter weather, and hunter harvest.

A predicted yield curve for the modelled population (Fig. 10) differs slightly from the quadratic form predicted by Caughley (1966), Ricker (1975) and McCullough (1979). The left side of the moose curve is characterized by a relatively straight-line relationship between sustainable harvest and

winter moose population size. Maximum sustained yield (MSY) was estimated to occur at 1,050 - 1,100 moose (0.7K). As population size increases above this level, yield decreases at an increasing rate. The region to the right of the apex in the yield curve (Fig. 10) has high stability (McCullough 1979) in that the standing population returns quickly when displaced by under- or over-harvesting. Management agencies should find this characteristic attractive but must, 1) be able to identify the ecological carrying capacity of the range and its long term trend, 2) have the ability to allow moose populations to grow above 0.7K, and 3) be able to estimate moose densities. Importantly, natural mortality can hold moose populations at densities well below the limits imposed by food resources alone. For example, high predation rates reduced MSY by 60% in Alaskan moose (Van Ballenberghe and Dart 1982). Simulated moose populations in their study that were harvested only slightly above MSY declined rapidly. Hunting was speculated to be additive at very low

Table 4. Calculations of compensatory hunting mortality rate on adult female moose. Simulation model was run with combinations of density and harvest rates.

| Density as fraction of (K) | Harvest rate ^a (%) | Total annual non-hunting mortality rate ^b (%) | Total annual mortality rate | | Compensatory mortality (A - B) |
|----------------------------|-------------------------------|--|-----------------------------|-----------------------------|--------------------------------|
| | | | Predicted ^c (A) | Calculated ^d (B) | |
| 0.30 | 7.0 | 16.9 | 23.9 | 23.9 | 0 |
| 0.69 | 1.4 | 16.7 | 18.1 | 17.9 | 0.2 |
| 0.78 | 1.4 | 18.2 | 19.6 | 18.4 | 1.2 |
| 0.96 | 4.2 | 22.9 | 27.1 | 24.1 | 3.0 |
| 1.03 | 2.8 | 23.8 | 26.6 | 23.9 | 2.7 |

^a Harvest rates were chosen from simulations in which density was similar to density in simulations with no hunting.

^b Harvest rate = 0%.

^c Total annual mortality rate (%) predicted if hunting mortality was completely additive.

^d Total annual mortality rate (%) calculated by model with indicated harvest rates.

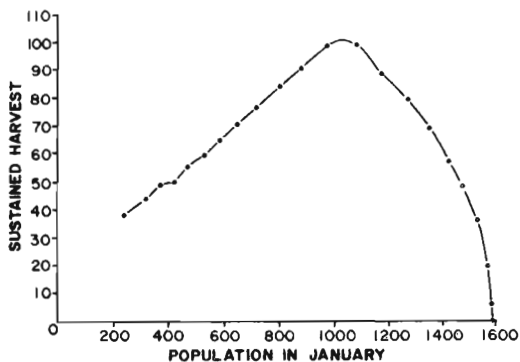


Figure 10. Predicted yield from a simulated moose population on a 2396 km² area of southeastern New Brunswick. Population in autumn was harvested at a rate of 0.11 annually.

harvest rates in their population because predation held the population below 0.7K and, as in New Brunswick, density-dependent processes associated with food limitation presumably did not function.

CONCLUSIONS

The model mimics well the current trend in population size and annual harvests of the real population on the study area. Model responses to perturbations in either mortality or natality appear biologically reasonable. Quantifying the role of hunting in the modelled population should then provide insight into hunting in the real population.

1. The simulated moose population is more sensitive to harvest rate if harvest is composed entirely of cows and calves than if the entire harvest was taken from the antlered segment.
2. Population rate of change (r) was not affected by the proportion of males in harvest above 60% regardless of harvest rate.
3. For southeastern New Brunswick, a harvest rate of 7%, with antlered males comprising 70-95% of the harvest, will provide maximum harvests.

4. Harvest rates greater than 10% during rut initiated a negative exponential rate of change in the simulated population. This harvest rate is moderate in comparison to the 24% taken from some heavily hunted areas in Quebec (Messier and Crête 1984). However, immigration from adjacent, lightly hunted populations helped maintain high harvest rates in those Quebec localities (Crête and Jolicoeur 1985).

5. Hunting moose after the rutting period allows a harvest rate 10% greater than before or during the rut.

6. The modelled population is sensitive to changes in recruitment, a function of both production and juvenile survival.

7. Hunting is an additive mortality on adult females at densities below 0.7K regardless of harvest rate. Harvest rates above 3% are additive at K.

In a natural system with predators such as wolves or bears and no hunting, one would expect moose population dynamics to be influenced primarily by the mortality rate (from predation) of juveniles. Recruitment to the population is then held at low levels. In the New Brunswick study area, hunting focused primarily on adult moose and predation losses were light; the number of juveniles recruited into the population was controlled by the number of breeding cows surviving and the ratio of adult bulls to cows.

Harvest rates greater than 10% are predicted to cause a population decline in the model. As the proportion of cows and calves in the harvest increased above 40%, the maximum allowable harvest rate (maintains $r \geq 0$) declined from 10%. For the real population, a harvest rate of 10% is lower than we expected in an environment characterized by relatively mild winters, limited black bear predation on calves, and no wolves. Furthermore, the calculated harvest rate of 7% on adult females in the real population is a small portion of the 25% annual mortality rate calculated for the study population (Boer 1988b). Consequently, moose populations in

southeastern New Brunswick appear to be driven by natural mortality factors and poaching of the adult cohort. These mortality factors set the limit of sustainable legal harvests.

Hunting losses are under the control of management agencies whose ability to manipulate populations is limited. The contour lines of the rate of change (r) nomogram are relatively wide apart (Fig. 8e), usually a safe policy area. Lines close together indicate regions of uncertainty where small changes in the values of driving variables yield large changes in system response. Hence, hunting in the modelled population is less efficient as a management tool than if the population could withstand a higher harvest rate.

Two problems in management of an exploited population are defining the expected yield as a function of population size and the difficulty in accurately and precisely calculating the standing population. Wide variability in estimates of population makes it prudent to manage populations within bounds where the population is most resilient. Curves of rate of change (r) were farthest apart at harvest sex ratios near 1:1 (Fig. 8e, curves A, B, and C). Artificially maintaining a wide disparity in sex ratio or age structure through hunting increases the risk of a catastrophic collapse in a natural, and variable, system.

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REFERENCES

- ANDERSON, D.R., and K.P. BURNHAM. 1976. Population ecology of the mallard. VI. The effect of exploitation on survival. U.S. Fish and Wildl. Serv., Resour. Publ. 128.
- BALLARD, W.B., T.H. SPRAKER, and K.P. TAYLOR. 1981. Causes of neonatal moose calf mortality in southcentral Alaska. *J. Wildl. Manage.* 45: 335-342.
- BOER, A.H. 1987. Hunting and the population dynamics of moose in New Brunswick. Ph.D. Thesis, Univ. of New Brunswick, Fredericton, N.B. 95pp.
- _____. 1988a. Moose calf mortality in New Brunswick. *Can. Field-Nat.* 102:74-75.
- _____. 1988b. Mortality rates of moose in New Brunswick: a life table analysis. *J. Wildl. Manage.* 52: 21-25.
- BISHOP, R.H., and R.A. RAUSCH. 1974. Moose population fluctuations in Alaska, 1950-1972. *Nat. Can.* 101: 559-593.
- BLOOD, D.A. 1974. Variation in reproduction and productivity of an enclosed herd of moose (*Alces alces*). *Proc. Int. Congr. Game Biol.* 11: 59-66.
- CAUGHLEY, G. 1966. Mortality patterns in mammals. *Ecology* 47: 906-918.
- _____. 1977. Analysis of vertebrate populations. John Wiley and Sons, London. 234pp.
- _____. 1979. What is this thing called carrying capacity? Pages 2-8 in M.S. Boyce, and L.D. Hayden-Wing, eds. North American elk: ecology, behaviour, and management. Univ. Wyoming, Laramie.
- CLUTTON-BROCK, T.H., F.E. GUINNESS, and S.D. ALBON. 1982. Red Deer - behaviour and ecology of two sexes. Univ. Chicago Press, Chicago. 378pp.
- CRÊTE, M., and H. JOLICOEUR. 1985. Comparing two systems of moose manage-

- ment for harvest. *Wildl. Soc. Bull.* 13: 464-469.
- _____, L.-P. RIVEST, H. JOLICEUR, J.M. BRASSARD, and F. MESSIER. 1985. Visibility bias and precision for moose density estimated from helicopter and fixed-wing aircraft in southern Quebec. Unpublished manuscript, Tourisme, Pêche et Faune, Quebec. 23pp.
- _____, R.J. TAYLOR, and P.A. JORDAN. 1981. Optimization of moose harvest in southwestern Quebec. *J. Wildl. Manage.* 45: 598-611.
- FRANZMANN, A.W., C.C. SCHWARTZ, and R.O. PETERSON. 1980. Moose calf mortality in summer on the Kenai Peninsula, Alaska. *J. Wildl. Manage.* 44: 764-767.
- GAVIN, T.A., L.H. SURING, P.A. VOHS, Jr., and E.C. MESLOW. 1984. Population characteristics, spatial organization, and natural mortality in the Columbian white-tailed deer. *Wildl. Monogr.* 91. 41 pp.
- GEIST, V. 1963. On the behaviour of the North American moose in British Columbia. *Behav.* 20: 377-416.
- GODDARD, J. 1970. Movements of moose in a heavily hunted area of Ontario. *J. Wildl. Manage.* 34: 439-445.
- HAUGE, T.M., and L.B. KEITH. 1981. Dynamics of moose population in north-eastern Alberta. *J. Wildl. Manage.* 45: 573-597.
- HOLLING, C.S. 1978. *Adaptive Environmental Assessment and Management.* John Wiley & Sons, New York. 377pp.
- HOUSTON, D.B. 1968. The Shiras moose in Jackson Hole, Wyoming. *Grand Teton Nat. Hist. Assoc. Tech. Bull.* 1. 110pp.
- JENKINS, R.P. 1987. Correlation of two winter severity indices with deer harvest statistics for west central New Brunswick. B.Sc.F. Individ. Proj. Univ. New Brunswick, Fredericton. 20pp.
- KEITH, L.B. 1974. Some features of population dynamics in mammals. *Proc. Int. Congr. Game Biol.* 11: 17-58.
- KELSALL, J.P. 1963. The moose, *Alces alces americana* (Clinton), of Fundy National Park, New Brunswick. Paper presented at 1963 N.E. Fish and Wildl. Conf., Portland, ME. 15pp. (Mimeographed).
- LARKIN, P. 1977. An epitaph for the concept of MSY. *Trans. Am. Fish Soc.* 106: 1-11.
- LERESCHE, R.E. 1974. Moose migrations in North America. *Nat. Can.* 101: 393-415.
- _____, and R.A. RAUSCH. 1974. Accuracy and precision of aerial moose censusing. *J. Wildl. Manage.* 38: 175-182.
- LYNCH, G.M. 1976. Some long range movements of radio tagged moose in Alberta. *Proc. North Am. Moose Conf. Workshop* 12: 220-236.
- MARKGREN, G. 1982. Moose populations along a climatic gradient across Sweden. *Nat. Swedish Environ. Protection Board Report.* 55pp.
- McCULLOUGH, D. 1979. *The George Reserve Deer Herd: population ecology of a K-selected species.* Univ. Mich. Press, Ann Arbor. 271pp.
- MESSIER, F., and M. CRÊTE. 1984. Body condition and population regulation by food resources in moose. *Oecologia* 65: 44-50.
- MOEN, A.N., and F. AUSENDA. 1987. Sensitive population parameters in modeling long-lived species such as moose. *Alces* 23: 33-47.
- PEEK, J.M. 1971. Moose - snow relationships in northeastern Minnesota. Pages. 39-49 in A.C. Haugen, ed. *Symposium on snow and ice in relation to wildlife and recreation.* Iowa State Univ. Press Ames.
- PETERMAN, R.M. 1975. New techniques for policy evaluation in ecological systems: methodology for a case study of pacific salmon fisheries. *J. Fish. Res.*

- Board Can. 32: 2179-2188.
- PETERSON, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. Natl. Park Serv. Sci. Monogr. 11. 210pp.
- PHILLIPS, R.L., W.E. BERG, and D.B. SINETT. 1973. Moose movement patterns and range use in northwestern Minnesota. J. Wildl. Manage. 37: 266-278.
- RICKER, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board. Can. Bull. 191. 382pp.
- ROUSSEL, Y.E., E. AUDY, and F. POTVIN. 1975. Preliminary study of seasonal moose movements in Laurentides Provincial Park, Quebec. Can. Field-Nat. 89: 47-52.
- SMITH, J.H., R. MCG. ARCHIBALD, and A.H. CORNER. 1964. Elaphostroglyosis in maritime moose and deer. Can. Vet. J. 5: 287-296.
- THOMPSON, I., and M.F. VUKELICH. 1981. Use of logged habitats in winter by moose cows with calves in northeastern Ontario. Can. J. Zool. 59: 2103-2114.
- VAN BALLEMBERGHE, V., and J. DART. 1982. Harvest yields from moose populations subject to wolf and bear predation. Alces 18: 258-275.
- _____, and J.M. PEEK. 1971. Radiotelemetry studies of moose in northeastern Minnesota. J. Wildl. Manage. 35: 63-71.
- VILKITIS, J.R. 1971. The violation simulation formula proves as reliable as field research in estimating closed-season illegal big game kill in Maine. Trans. N.E. Wildl. Conf. 28: 141-144.
- WATT, K.E.F. 1968. Ecology and resource management. McGraw-Hill, New York. 450pp.