HUNTING PRESSURE AND RATE OF INCREASE OF A MOOSE POPULATION AT A DENSITY BELOW CARRYING CAPACITY

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ABSTRACT: From 1980 to 1984, 54,000 hunting days were spent and a total of 758 moose (*Alces alces americana)* were harvested within 5 experimental blocks ranging from 539 - 1,257 km^2. Those blocks were located in central Québec between 45 - 150 km north of Trois-Rivières. A block of 544 km^2 was added to monitor a moose population in the absence of hunting. Hunting pressure was unequally distributed within the 5 blocks (0.7 - 6 hunting days / km^2), whereas hunting effort (hunting days / capture) ranged from 21 - 115 during the same period. The relationship between finite rate of increase (λ) of moose populations, derived from aerial moose counts conducted at the beginning and at the end of the study, and hunting pressure, led us to observe that the moose population began to decrease when hunting pressure exceeded 2.8 hunting days / km^2, but it increased at a rate of 21% without hunting pressure. A negative correlation also existed between hunting pressure and the mean age of moose harvested.

Key words: *Alces alces*, density, finite rate of increase, hunting effort, hunting pressure, moose, Québec

RÉSUMÉ: De 1980 à 1984, une activité de chasse totalisant 54,000 jours-chasseur a permis de récolter 758 orignaux (*Alces alces americana*) dans 5 blocs expérimentaux d'une superficie variant entre 539 et 1,257 km^2. Ces blocs étaient situés dans le centre-sud du Québec à une distance de 45 - 150 km au nord de Trois-Rivières. Par ailleurs, un bloc de 544 km^2 a été ajouté dans le but de mesurer la tendance d'une population d'orignaux en absence de chasse. La pression de chasse exercée était différente d'un bloc à l'autre (0.7 à 6 jours-chasseur/km^2) alors que l'effort de chasse (jours-chasseur/capture) a varié de 21 à 115 durant la même période. La relation entre le taux fini d'accroissement (λ), calculé à partir d'inventaires aériens réalisés au début et à la fin de l'étude, et la pression de chasse, a permis de constater que la population d'orignaux commençait à décroître lorsque la pression de chasse excédait 2.8 et qu'elle augmentait au taux annuel de 21% en absence de chasse. Nous avons également noté que l'âge des animaux récoltés diminuait avec l'augmentation de la pression de chasse.

Mots-clés: *Alces alces*, densité, effort de chasse, orignal, pression de chasse, Québec, taux d'accroissement fini

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Québec supports the highest hunting pressure (2.8 hunting days / km^2) for moose (*Alces alces*) in North America, with an average of 132,000 licenses for moose issued between 1980 and 1984 (Roy 1986, Crête 1987). On the north shore of the St. Lawrence River, wolf (*Canis lupus*) and black bear (*Ursus americanus*) are sympatric with moose populations which stabilize at a density of ~ 0.4 animals / km^2 when un-hunted (Messier and Crête 1985). Using field data and computer simulations, Crête *et al.* (1981) attempted to optimize moose harvest in southwestern Québec. To improve moose management in southwestern Québec, they recommended keeping moose density at about 0.2 moose / km^2 by regulating hunting pressure to about 2 hunting days / km^2. The precision of their model relied on the accuracy of aerial moose surveys which did not account for missed animals. By manipulating hunting pressure within 6 experimental blocks and monitoring changes in the number of moose within each block at 4-year intervals, we hypothesized that it could be possible to assess the optimal hunting pressure and optimal harvest for populations of moose living at a density below carrying capacity (*K*).

STUDY AREA

Our study area was located in Hunting Zone 15 in central Québec, approximately 45 - 150 km north of Trois-Rivières (Fig. 1). The relief is rolling hills with elevations ranging from 300 - 500 m. Lakes, ponds, and creeks are common and well distributed. Annual precipitation is 900 mm, with snowfalls corresponding to 25% of the annual precipitation. Mean temperatures in January and July are -12.5° C and 20° C, respectively, and the growing season ranges between 160 - 180 days (Wilson 1971).

The southern part of the study area is dominated by the Great Lakes and St.Lawrence River forest region, while the northern part is characterized by the Boreal forest (Rowe 1972). Balsam fir (*Abies balsamea*), mountain maple (*Acer spicatum*), sugar maple (*Acer saccharum*), and beaked hazel (*Corylus cornuta*) are the most common browse species available (Audy 1974, Vallée *et al.* 1976). Balsam fir, white spruce (*Picea glauca*), and black spruce (*P. mariana*) provide the most coverage in the study area, which overlaps 2 of the most productive moose ranges in Québec (Brassard *et al.* 1974). Moose, wolf, black bear, and a few white-tailed deer (*Odocoileus virginianus*) are the most common large mammals inhabiting the area. Except for moose, however, their density is unknown (Crête and Joly 1981).

Accessibility throughout the area is provided by a well-developed network of forest roads. In La Mauricie National Park (NP-0), hunting has been prohibited since 1971, whereas in the Mastigouche Game Reserve (MGR), a controlled moose hunt was first implemented in 1973 in accordance with the procedure described by Bouchard and Moisan (1974). In the 2 controlled harvest zones (ZECS), Chapeau-de-Paille (Z-4) and Borgia (Z-6), the access was limited to holders of a membership card who paid a flat rate for moose hunting. All experimental blocks were located in provincial Hunting Zone 15 where an either-sex moose regulation prevailed.

METHODS

The effect of hunting pressure on the post-harvest population of moose was measured within 6 blocks including NP-0 where hunting was not allowed. Blocks were selected according to their geographical proximity, topography, and relative homogeneity of forest canopy, to minimize all variations except hunting pressure. All but 1 block were approximately 540 km^2. The block Z-4, with 1,257 km^2, was selected to minimize the effect of moose dispersal from higher to lower density areas (Goudreault 1980).

The MGR, which was moderately hunted until 1979, was equally divided into 3 blocks (M-1, M-2, and M-3) within which the expected hunting pressure was aimed at 1, 2, and 3 hunting days / km^2, respectively. In each block, hunters were required to annually report the duration of their stay regardless of their success. In 1982, for reasons beyond our control, hunting pressure was not recorded in block Z-4.

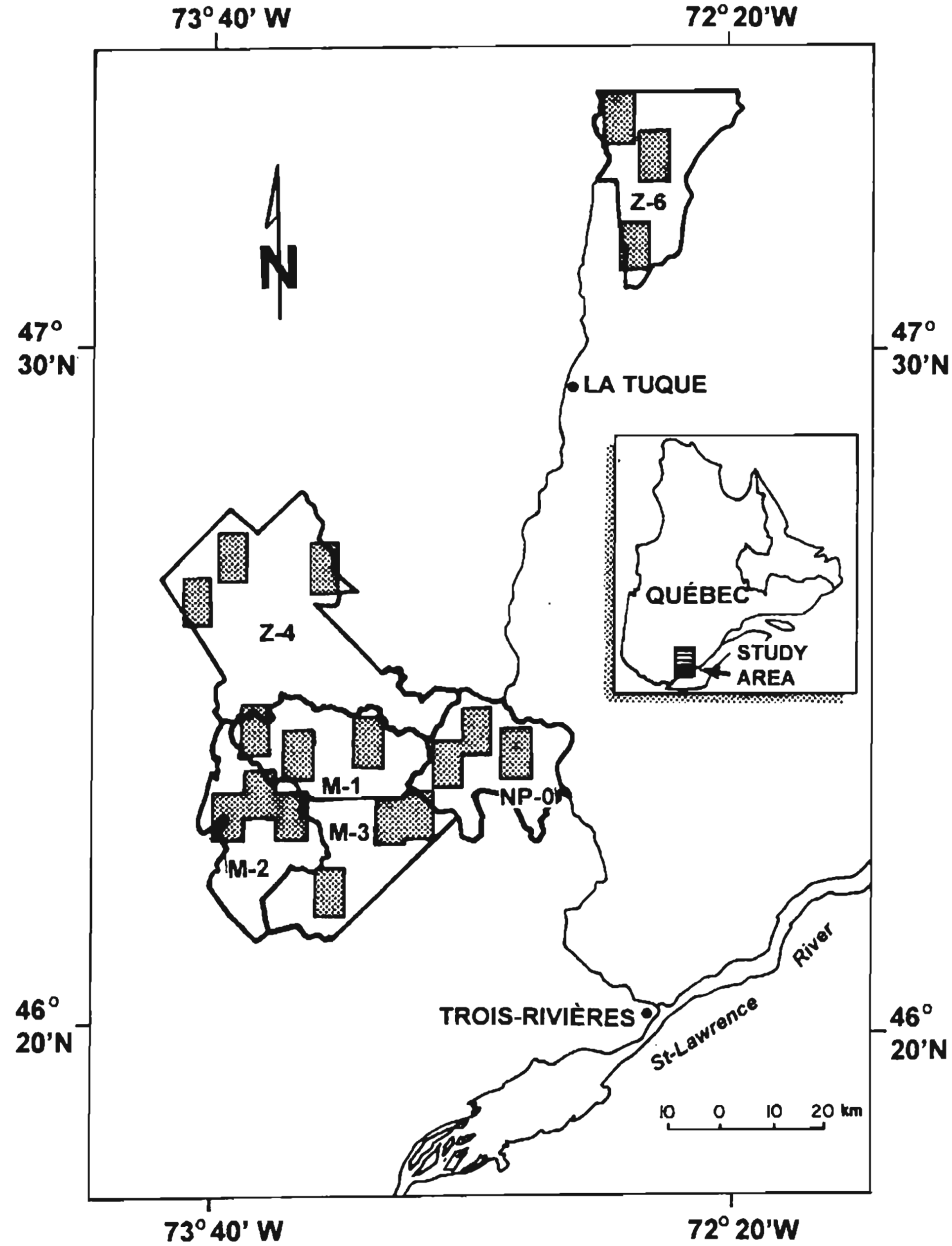

Fig. 1. Study area showing blocks and plots of 60 km^2 (6 x 10 km) used to monitor changes in moose population in central Québec (1980-1984).

The age of moose killed was determined by counting *cementum annuli* of the first incisor root (Sergeant and Pimlott 1959). The effect of hunting pressure was evidenced by regressing mean age of adult moose harvested per block against hunting days/km^2. The likelihood ratio Chi-square (SAS Institute 1987: 519-548) was also used to detect if differences existed in the proportion of yearlings and moose $\geq$ 10.5-

years-old between blocks.

Trends in moose populations were monitored, after the first and the last hunting season, by aerial surveys in accordance with the method described by Crête and St-Hilaire (1979). Three permanent plots of 60 km^2 randomly distributed without overlaps within each block were surveyed. Briefly, each plot was first flown with a fixed-wing aircraft (De Havilland Beaver) along north-south transect lines 500 m apart, at a mean altitude of 200 m. Two observers sat behind the pilot and reported to the navigator the number of moose sighted as well as the associated old and fresh track networks. For the second part of the survey, a helicopter with a navigator-observer and an observer sitting behind the pilot returned to the same plot to count and determine the sex of moose in each moose yard. Due to the low density of moose within heavily hunted blocks, moose located near the random plots were also sexed and categorized according to their maturity, leading to a larger sampling of the population.

Unfortunately, climatic and budget constraints prevented us from continuing the moose survey in Block Z-4 in 1981. During the following winter, Z-4 was surveyed with only a fixed-wing aircraft. To assess the number of moose within the 3 plots, equation models elaborated by Crête *et al.* (1986) were used to predict helicopter counts of moose. Sex of adult moose was ascertained by vulval patch and antlers and, in a few instances, by the color of the snout (Roussel 1975, Crête and Goudreault 1980). Calves were identified by their relative size, but no attempt was made to determine their sex. Confidence intervals ($\alpha = 0.10$) associated with ratios were calculated using the method of Czaplewski *et al.* (1983). We used the likelihood ratio Chi-square procedure to determine if mean age of adult moose and the ratios (males:100 females and calves:100 females) of moose harvested differed among blocks or for the post-hunted moose population, among survey years and blocks.

Overall densities of moose in 1981 and 1985, for blocks subjected to hunting, were estimated by stratified random sampling, and confidence intervals were calculated at $\alpha = 0.05$ (Cochran 1963: 87-95). The number of moose between aerial surveys was compared using the Wilcoxon matched-pair signed-rank test (Siegel 1956). To meet the minimum sample size required ($n = 6$ at $\alpha = 0.05$), blocks were paired by increasing order of hunting pressure (NP-0 with M-1, M-2 with M-3, and Z-4 with Z-6).

Two methods were used to assess the optimal hunting pressure. First, if a relationship between hunting pressure and finite rate of increase for the moose population in each block existed, we expected to find the optimal hunting pressure corresponding to a rate of increase of 1.0. Second, if the overall density of the moose population remained the same in hunted blocks during the study period, sustainable yield and hunting pressure could be derived from hunting parameters. The sustainable yield and the optimal hunting pressure are respectively provided by the yearly average of moose harvested or the yearly average of hunting days divided by the total area of hunted blocks.

RESULTS

Hunting Pressure and Hunting Effort

From 1980 to 1984, 54,000 days were spent by moose hunters within the 5 hunted blocks. Except for NP-0, hunting pressure varied from 0.7 - 6.0 hunting days / km^2, whereas hunting effort ranged from 21 - 115 hunting days / moose during the same period (Table 1). The hunting effort was more variable than the hunting pressure, as evidenced by the coefficient of variation. Only Z-4 and Z-6 had hunting pressure and hunting effort exceeding those of Manage-

Table 1. Parameters of moose hunting on 5 experimental blocks located in central Québec (1980 - 1984). HP = hunting pressure (hunting days/km²); HE = hunting effort (hunting days/capture).

	Experimental blocks									
	M-1 (539 km²)		M-2 (539 km²)		M-3 (539 km²)		Z-4[1] (1,257 km²)		Z-6 (546 km²)	
Statistics	HP	HE	HP	HE	HP	HE	HP	HE	HP	HE
$\bar{X}$	0.7	20.9	1.8	51.9	2.6	45.7	3.8	97.2	6.0	115.6
SD	0.1	11.9	0.24	18.0	0.28	3.94	0.52	19.99	1.69	48.76
Range	0.6-0.8	6.7-38.2	1.4-2.0	34.3-78.0	2.1-2.8	40.1-51.2	3.6-4.3	91.6-125.7	4.1-8.5	72.2-193.7
CV	11	51	12	31	10	8	12	21	25	38

[1]Data not available in 1982

ment Zone 15, estimated at 3.3 hunting days / km² and 64 hunting days / moose, respectively (IQOP 1985).

Harvest

A total of 758 moose were harvested during the study period (Fig.2). The block Z-4 accounted for the largest number of moose killed, whereas M-3 provided the mean highest yield per 10 km². Only M-1 showed a slight positive trend when moose crop was regressed against years (P = 0.09).

We determined the age of 358 moose harvested over 5 years (Table 2). Hunting pressure influenced the mean age of moose harvested during this period: hunting pressure was negatively correlated with age (r = -0.99, $P < 0.01$). The proportion of yearling males in the harvest did not change between blocks ($P = 0.233$), but differences in proportions were evidenced for moose $\geq$ 10.5-years-old if males and females were pooled ($P = 0.099$). The sex-ratio of adult moose in the harvest favored males, except in M-2. A positive trend ($r = 0.95, P < 0.05$), related to an increase in hunting pressure, occurred for calves:100 females in the harvest.

Density, Sex-ratios, and Productivity of Moose Populations

Two years before the initiation of the study, densities were measured in all blocks but Z-6 (Goudreault and Milette 1984). Moose densities were under 4.0 moose / 10 km², which corresponded to the carrying capacity (K); i.e., the level at which a low-density equilibrium was observed in southwestern Québec (Messier and Crête 1985).

The first aerial survey indicated an adult sex ratio of 50:50 ($P > 0.05$), while NP-0, M-1, and M-2 departed from theoretical parity ($P < 0.05$) at the end of the project (Table 3). Changes in sex-ratio in favor of females were observed between years only in M-2 ($P < 0.05$). Productivity within blocks (calves:100 adult females) remained unchanged between years ($P > 0.10$), whereas noticeable variations among blocks occurred during the second aerial survey ($P = 0.003$).

High and low hunting pressures resulted in fluctuations of post-hunted moose populations (Table 4). Blocks were paired by increasing order of hunting pressure (NP-0 with M-1, M-2 with M-3, and Z-4 with Z-6) and tested for differences in the number of moose between aerial surveys in each plot of 60 km². We observed an increase in the first pair ($P < 0.05$), stability

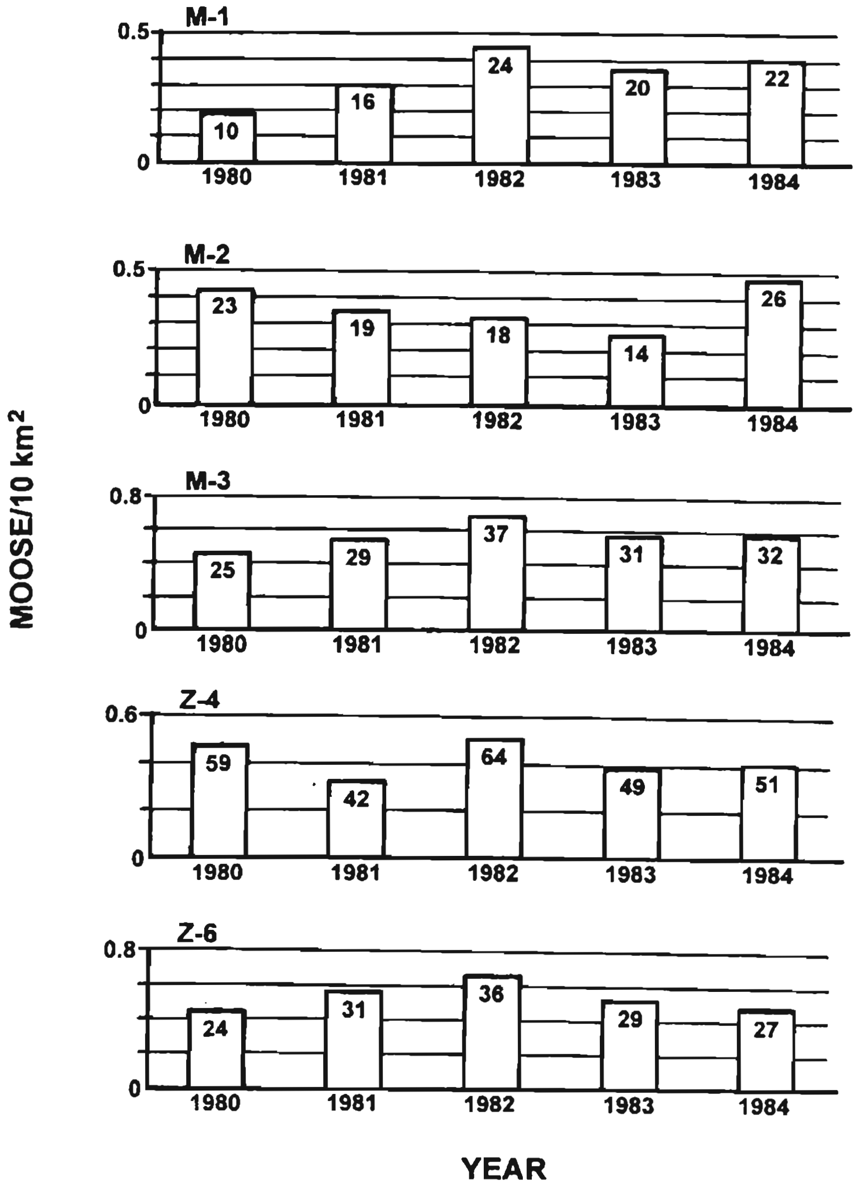

Fig. 2. Number of moose harvested / 10 km² in each block between 1980 and 1984 in central Québec. The value in each bar corresponds to the number of moose harvested for that year.

in the second ($P > 0.05$), and a decrease in the third pair ($P < 0.05$).

Hunting Pressure and Optimal Harvest

Hunting pressures drastically influenced the finite rate of increase of moose populations: this population parameter stabilized at a hunting pressure of 2.8 hunting days / km², whereas it increased at an annual rate of 21% in the absence of hunting (Figure 3).

The overall densities for the 5 hunted blocks, after corrections for missed animals were made (Crête *et al.* 1986), remained the same as indicated by the first and the second survey (e.g., 0.32 moose / km² ±

Table 2. Mean age (SD; *n*) of adult moose and the ratios (males : 100 females and calves : 100 females) of moose (*n*) harvested under different hunting pressure during 5 years (1980-1984). Blocks Z-4 and Z-6 are pooled for age.

Block	Age (years)			Ratios	
	M	F	M + F	M:100 F	C : 100 F
M-1	6.4 (4.26; 45)	6.3 (5.05; 27)	6.4 (4.81; 72)	141 (89)	8 (40)
M-2	4.2 (2.55; 43)	6.4 (509; 43)	5,3 (4.15; 86)	100 (96)	8 (52)
M-3	4.2 (3.14; 71)	4.9 (3.72; 49)	4.5 (3.40; 120)	147 (141)	23 (70)
Z-4				124 (240)	23 (132)
Z-6				133 (128)	35 (74)
Z-4 + Z-6	3.8 (2.83; 48)	4.0 (3.35; 32)	3.9 (3.03; 80)		

20% vs. 0.33 moose / km^2 ± 28%).

Considering the total of 54,000 days spent over 5 years in hunted blocks (3,420 km^2), a yearly average of 3.2 hunting days / km^2 was reached, allowing a harvest of 0.044 moose / km^2.

DISCUSSION

Hunting pressure was better controlled in M blocks, due to the limited access and number of hunting days per hunting party. Hunting effort may be influenced by moose density (Crête *et al.* 1981), climatic conditions, and the hunter's level of skill. Crête (1987) reported a tendency of hunters to be more selective when moose density was high. This hunter behavior results in a higher effort in hunting for particular sex and age classes of moose. Because practically all the blocks were concentrated in the same area, climatic variations among blocks during the hunting season were eliminated. Finally, we assumed that hunters were equally skilled.

The overall density for the 6 blocks remained the same as indicated by the first and second aerial surveys (0.32 vs. 0.33 moose / km^2). Moose populations increased in blocks subjected to low hunting pressure, but where hunting pressure was high, de-

Table 3. Sex ratio [adult males / 100 adult females (CI[1]; *n*)] and productivity index [calves / 100 adult females (CI[1]; *n*)] in post-hunted moose populations surveyed during winters of 1981 and 1985.

Block	Sex ratio		Productivity	
	1981	1985	1981	1985
PN-0	89 (39.7; 36)	39 (17.2; 50)	30 (18.7; 26)	14 (9.5; 41)
M-1	48 (23.7; 40)	32 (12.2; 75)	33 (18.8; 36)	35 (13.0; 77)
M-2	89 (44.6; 36)	41 (17.1; 58)	9 (10.0; 24)	7 (6.2; 44)
M-3	83 (53.8; 22)	73 (43.4; 26)	38 (30.7; 18)	40 (28.4; 21)
Z-4	72 (28.2; 67)	100 (60.9; 28)	46 (17.0; 57)	43 (34.4; 20)
Z-6	50 (24.2; 42)	30 (29.3; 13)	41 (20.7; 41)	90 (61.7; 19)

[1]$\alpha = 0.10$

Table 4. Number of moose counted in each plot of 60 km² after the first and the last hunting season of the project (1980-1984), as well as the finite rate of increase (λ) of the moose population derived from the time interval.

Block	Hunting pressure[1] (hunting days/km²)	Moose survey 1st	Moose survey 2nd	Interval (year)	Finite rate of increase (λ)
PN-0	0			4	1.20
$\bar{X}$		9	18.7		
SD		10.8	6.1		
Range		0-21	12-24		
M-1	0.7			4	1.15
$\bar{X}$		16.3	28.3		
SD		8.3	5.7		
Range		7-23	22-33		
M-2	1.9			4	1.06
$\bar{X}$		14.7	18.7		
SD		7.0	2.3		
Range		8-22	16-20		
M-3	2.7			4	1.03
$\bar{X}$		9.3	10.7		
SD		5.67	1.53		
Range		3-14	9-12		
Z-4	3.4			3[2]	0.95
$\bar{X}$		13.3	11.3		
SD		4.16	6.51		
Range		10-18	5-18		
Z-6	5.3			4	0.79
$\bar{X}$		18.7	7.3		
SD		8.74	1.53		
Range		9-26	6-9		

[1]Mean hunting pressure was calculated for years subsequent to the first survey

[2]First aerial survey was made 1 year later for Z-4

creases occurred. As a consequence of population growth, a slight increase in the number of moose harvested during the study period was noted only in M-1. The number of moose harvested, however, did not change when moose density was reduced, (e.g., Z-

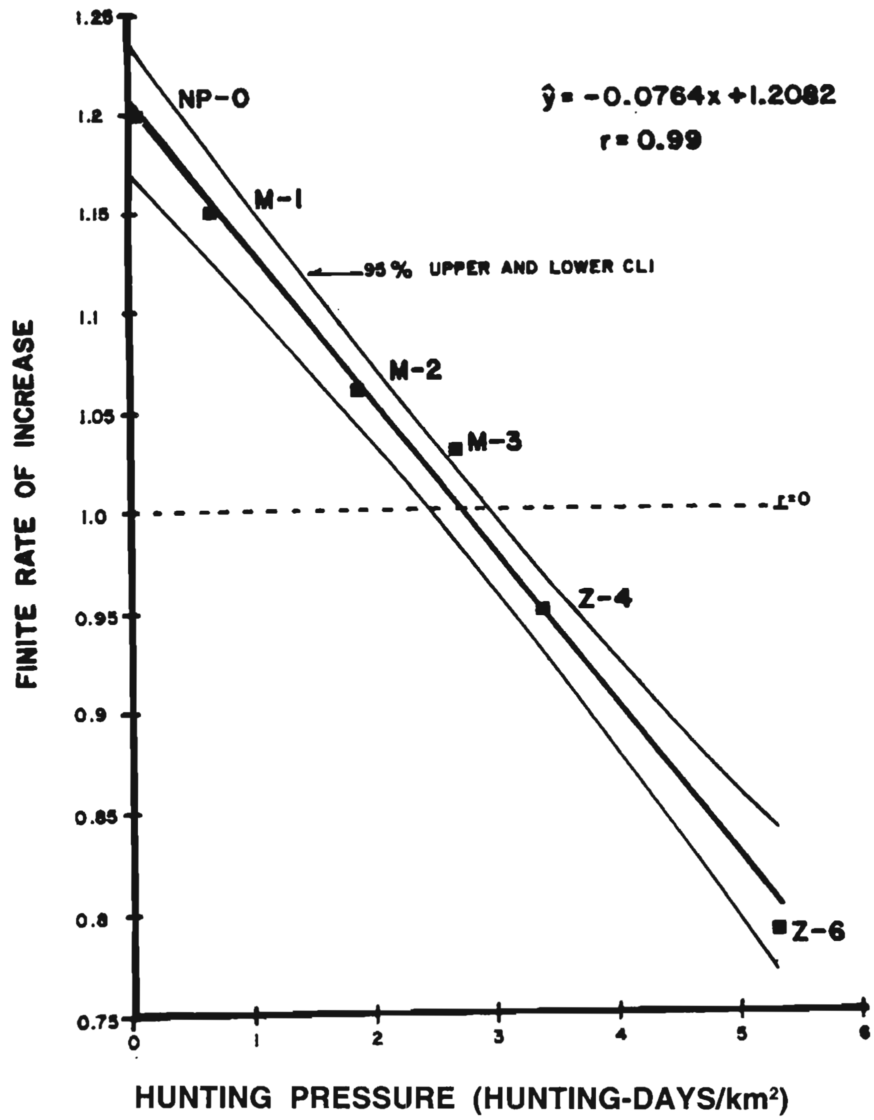

Fig. 3. Relationship between the finite rate of increase (λ) of moose population and the hunting pressure (hunting days / km^2) in central Québec (1980-1984). The dashed line represents a stable population that corresponds to the exponential rate of increase of r = 0.

4 and Z-6), most likely because hunters unreacted by increasing their searching effort.

Changes in moose density were also reflected by changes in the mean age of moose harvested. Age is commonly used in conjunction with other harvest parameters to assess trends in moose populations (Crichton 1992). Our results suggest that the mean age of moose observed (i.e., under 4 years old) may indicate an overharvested population.

Changes in sex-ratio in the population of moose between surveys occurred in only 2 blocks (NP-0 and M-2). There was no hunting in NP-0, whereas an equal sex-ratio in adult moose occurred in M-2. These results could be explained by sampling bias or, more likely, by adult males leaving the blocks NP-0 and M-2 located on either side of M-3, which was subjected to a higher hunting pressure. Moreover, NP-0 and M-2 were bordering provincial Hunting Zone 15 where hunting pressure was 3.3 hunting days / km^2 in 1984 (IQOP 1985). Egress of adult males can be explained by their wandering during summer or even during the hunting season when males are lured by hunters imitating female vocalizations. Movements of moose from higher to lower density has also been documented for parks and wildlife reserves in Québec, but the effect of moose dispersal was limited within a 5-km band surrounding lightly harvested areas (Goudreault 1980, Labonté *et al.* 1998).

On the other hand, the overall calf:cow ratio remained stable between years, but variations among blocks occurred in 1985. Blocks M-2 and NP-0 contributed the most to these changes. For unknown reasons, productivity in M-2 remained steadily low in both surveys. Messier and Crête (1985), who studied the moose-wolf dynamics in 3 areas supporting different moose densities, concluded that wolves may adjust their numerical and functional responses in relation to prey densities and, consequently, year-long rates of predation were density-dependent, increasing from 6.1% to 19.3% as moose density increased from 0.17 to 0.37 moose / km^2. At those densities, the numbers of calves per 100 females were 65 and 37, respectively.

In this study, hunting pressure caused changes in moose density for at least 2 groups of paired blocks. In NP-0 and M-1, where the number of moose increased, and also in Z-4 and Z-6, where the number of moose decreased. The densities estimated within paired blocks in winter 1985 were 0.54 moose / km^2 (NP-0 + M-1), 0.33 / km^2 (M-2 + M-3), and 0.21 / km^2 (Z-4 + Z-6), and the number of calves per 100 females were, respectively, 27, 16, and 63, in spite of a greater number of calves harvested in the latter paired blocks. Our results are clouded by the low chronic productivity observed in M-2 and by the changes in moose density taking place in a relatively short time, forcing wolves to deal with a new situation, which has not yet been documented.

Our results clearly indicate the high potential of moose populations in recovering from low density when hunting is prohibited (e.g., NP-0) and, conversely, density may collapse rapidly if excessive hunting pressure is maintained as in Z-6. Fortunately, moose cannot be extirpated easily from a large area because the effort needed would be so intense that hunters would lose their interest in hunting before this occurred (Crête *et al.* 1981).

Courtois and Jolicoeur (1993) studied changes in moose harvest per unit of effort in several parts of Québec. For central Québec, they recommended an optimal effort of 3.1 hunting days / km^2 for harvesting moose at 0.045 moose / km^2. These recommendations reflected our findings; i.e., 3.2 hunting days / km^2 and 0.044 moose / km^2. On the other hand, the relationship between finite rate of increase and hunting pressure indicated an optimal hunting pressure of 2.8 hunting days / km^2, which is more conservative.

Carrying capacity (K) of the moose habitat may be expressed in terms of food and predation. In absence of wolves, (e.g., south of the St. Lawrence River), K has been approximated to 2.0 moose / km^2, but it is 0.4 moose / km^2 in southwestern Québec where moose populations are regulated by wolves (Crête 1989, Messier 1994). Therefore, density providing MSY is 0.6 K; i.e., 0.24 moose / km^2 (Crête 1987).

The overall densities estimated in hunted blocks during this study corresponded to 0.8 K which, in theory, precludes the maximum sustained yield. The lack of precision of our moose surveys prevents firm conclusions, but results from this study should be regarded as guidelines to help moose managers in setting the optimal hunting pressure if non-selective harvest is the rule. These results are valid for moose populations of central Québec living at a density below carrying capacity in a system without alternate prey like the white-tailed deer.

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