

PREDICTING MOOSE POPULATION PARAMETERS FROM HUNTING STATISTICS

Réhaume Courtois¹ and Michel Crête^{1,2}

¹ Ministère du Loisir, de la Chasse et de la Pêche, Service de la faune terrestre, 150 Boul. René-Levesque est, Québec, Qué., G1R 4Y1 ² Centre d'études nordiques, Université Laval, Sainte-Foy, Qué., G1K 7P4

ABSTRACT: We developed six regression models predicting density, harvest rate, % calves in autumn, annual rate of increase, and number of males and calves per 100 females in winter, based on 52 aerial surveys related to 10 hunting statistics. The 6 models were statistically significant but predictions for densities and harvest rates had higher R^2 (0.74-0.68) than the 4 other predicted variables (0.23-0.52). We are confident that predicted population parameters are adequate for managing moose populations. They are straightforward and easier to interpret than the traditional hunting statistics used up until now for annual monitoring of moose populations. Regression models made it possible to reconstruct population parameters for the 1971-1992 period even if routine aerial censuses only began in the mid-eighties. Predictions appeared less precise for some hunting zones, particularly for southern Québec where few aerial surveys were available to construct regression models.

Five homogeneous groups of hunting zones (and moose populations) were delineated by cluster analysis applied to hunting statistics. Southern populations were characterized by high productivity and low densities, due to intense harvest rates. Southwestern populations were the least productive but, due to high densities, had relatively high yields per surface area. Northern populations were characterized by very low densities, low productivity and low harvest rates. Central and north-central populations exhibited intermediate characteristics. These results indicate that it will be necessary to develop independent models for each group of hunting zones to improve the accuracy of the predictions when sufficient data becomes available.

RÉSUMÉ: Nous avons développé six modèles de régression multiple permettant de prédire la densité, le taux d'exploitation, le % de faons à l'automne ainsi que le nombre de mâles et de faons / 100 femelles à l'hiver en utilisant les résultats de 52 inventaires aériens et en employant les statistiques de chasse comme variables indépendantes. Les 6 modèles étaient significatifs mais la densité et le taux d'exploitation présentaient des R^2 plus élevés (0,74-0,68) que les 4 autres variables dépendantes. Nous croyons que les paramètres prédits sont adéquats pour faire le suivi des populations d'originaux. Ils sont précis et plus faciles à interpréter que les statistiques de chasse utilisées jusqu'à présent pour gérer l'original. Les régressions multiples ont permis de reconstruire les paramètres des populations pour la période de 1971 à 1992 même si les inventaires aériens de routine ne sont effectués que depuis le milieu des années 1980. Les prédictions semblent moins précises pour certaines zones de chasse, particulièrement celles du sud du Québec, où peu d'inventaires étaient disponibles pour construire les modèles de régression.

Cinq groupes de zones de chasse (et de populations d'originaux) ont été délimitées par analyse de groupement appliquée aux statistiques de chasse. Les populations du sud du Québec sont caractérisées par une forte productivité mais des faibles densités à cause d'un taux d'exploitation élevé. Dans le sud-ouest de la province, les populations sont peu productives mais leurs rendements par unité de surface sont élevés grâce à des densités fortes. Les populations nordiques se caractérisent principalement par de très faibles densités, une productivité réduite et des taux d'exploitation bas. Les populations du centre et du centre-nord possèdent des caractéristiques intermédiaires. Ces résultats montrent qu'il serait nécessaire de développer des modèles indépendants pour chaque groupe de zones afin d'accroître la précision des prédictions lorsque suffisamment de données seront disponibles.

ALCES VOL. 29 (1993) pp.75-90

Wildlife managers evaluate the impact of sport hunting on animal populations to define biological, social and economic objectives, and to take appropriate measures to meet such objectives. Approaches may differ from one jurisdiction to the next depending on target objectives, population status or characteristics and the socioeconomic context. Direct methods, of which aerial surveys are the best example, involve counting animals. Such methods give easily interpretable results but involve major problems such as prohibitive costs, relative inaccuracy and bias related to unobserved animals (Crête *et al.* 1986, Gasaway and Dubois 1987). These problems have led most agencies to rely on indirect methods such as pellet group counts, vehicle collisions, track abundance, or biological indices: mean age, % males, % yearlings. These methods are correlated to population characteristics and can provide population trends. Their greatest weaknesses are their inability to give absolute results (population size, composition, etc.), their dependence on extrinsic parameters (hunting conditions, weather, etc.), their sensitivity to sampling errors (Courtois 1989) and the complexity in interpreting conflicting indices (Fryxell *et al.* 1988).

The moose (*Alces alces*) management system in Québec relies on three sources of information. Since 1971, demographic trends (abundance, sex ratio, recruitment, mean age) have been monitored using hunting statistics collected at some 275 registration stations. Historically, hunting effort has been estimated by mail surveys conducted at five-year intervals; since 1989, however, a complete census of hunters has been made possible by means of licenses specific to each management unit. Finally, aerial surveys (Courtois 1991a), instituted in 1987, have allowed the estimation of herd size and composition in each management unit at five-year intervals.

The current system seems to correctly describe population changes of moose in Québec (Courtois and Lamontagne 1990).

Recently, emphasis has been put on aerial surveys because they can give the most precise image of a population (Timmermann 1974, Gasaway and DuBois 1987). Moreover, results obtained from these surveys directly (densities, herd sizes, productivity indices) or after conciliation with hunting statistics (harvest rates, recruitment, etc.), are easy to interpret because they refer to absolute numbers. Unfortunately, the costs and manpower involved do not permit more than one survey every five years in each Québec hunting management unit. Between two surveys, the population status must be determined by means of hunting statistics. Those later data were not given sufficient consideration. Historical data have been computerized since 1971 and were only used to meet their initial objective: to describe population changes at the management unit scale without any reference to surrounding units. A more global analysis would make it possible to identify relations between hunting statistics and aerial surveys data as well as an identification of groups of management units with similar population characteristics, thus allowing similar management strategies.

Our work has two objectives: (1) to develop regression models that can predict population parameters based on hunting statistics similar to Crête and Dussault (1986) and, (2) to use hunting statistics to identify discrete populations showing similar characteristics.

METHODS

Hunting statistics

Hunting statistics came from annual reports drawn from the «Big Game Information System» data base (Gauthier and Roy 1981; Roy 1985; Breton 1991; Bouchard 1990). Since 1958, hunters in Québec must report their kills at the end of their hunting trip. Historical series include the date and length (days) of the hunting season and 10 indices used to describe changes in abundance, productivity and harvest rates (Courtois 1989).

Table 1 gives the definition of each variable as well as the methods used to compute them.

Aerial surveys

Aerial surveys are used in Québec to estimate moose density (moose/10 km² of habitat), total population size per hunting zone and population composition (% of males among adults; calves/100 females). The surveys are carried out in 2 phases (Crête *et al.* 1986; Courtois 1991b) using 60 km² sampling plots. In the first phase, moose track networks visible in the snow are mapped by flying north-south transects at 500 m intervals. This is done using airplanes or helicopters flying at 160 km/h at an average altitude of 110 m above the ground. In the second phase, track networks are flown over at low altitude using helicopters to count and classify moose (calves, adult males and females) (Crête and Goudreault 1980). Phase 2 can be carried out in all (stratified random sampling; Snedecor and Cochran 1971) or a fraction (25-66%) of the sampling plots covered in phase 1 (double sampling; Rivest *et al.* 1990). In double sampling, the total population and its variance are estimated using regression models making it possible to predict the number of moose present in a track network on the basis of its surface area and on the number of moose seen during phase 1. In all cases, the estimated densities are corrected for visibility bias using 0.73 for visibility rate (Crête *et al.* 1986).

The data base used in this study comes from 52 aerial surveys carried out in various hunting zones of Québec between 1976 and 1991. Surveys prior to 1986 were taken from Crête and Dussault (1986), whereas the most recent are described by Courtois (1991a). Results of aerial surveys were associated with hunting statistics observed during the autumn preceding each survey (Table 1). In addition to density and winter composition, it was possible to calculate harvest rate, percentage calf in autumn (Caughley 1974) and an index of the rate of increase of the population

(Bergerud and Elliot 1986) assuming absence of natural mortality.

Mail surveys

The activity of hunters was evaluated by mail surveys (Pelletier and Therrien 1977, 1978; Lacasse and Pelletier 1979; Statbec 1984; IQOP 1985; Nedelca 1991). Two indices, the hunting pressure and the hunting effort, were chosen to estimate hunter effort (Table 1).

Statistical analyses

The data were processed using the SAS software package (SAS Institute 1987). Multiple linear regressions (REG/Stepwise procedure; SAS Institute 1987) were computed in order to predict, on the basis of hunting statistics, the six population parameters (density, harvest rate, % calves, rate of increase, males and calves/100 females) as estimated during aerial surveys. The calf sex ratio was excluded from this analysis because of too many missing values. The other 9 hunting statistics were used as were their naperian logarithmic and square root transformations to detect non-linear relations (Legendre and Legendre 1979: 13). The longitude and the latitude at the central point of each hunting zone were also submitted to the regressions to take into account regional variations. Only those independent variables significant to a level of $P \leq 0.10$ were retained in the final models.

Reliability of the regressions was tested by cross-validation (Crête *et al.* 1986). Fifty-two regression models were computed with each one excluding a different survey. Values observed during a given aerial survey were then predicted using the models that were computed without data from that given survey. There was then complete independence between observed and predicted values. We determine the presence of bias by comparing predicted variables with those measured in the 52 aerial surveys. We also estimated the

TABLE 1 .Variables used in the analysis and methods employed to compute them.

VARIABLE	DEFINITION	DESCRIPTION
HARVEST STATISTICS		
Abundance indices		
HARVEST	Number of moose recorded at the registration stations	
HAR_10KM	Harvest by 10 km ² of moose habitat in each hunting zone concerned	$\frac{\text{HARVEST}}{\text{habitat area (km}^2\text{)}} \times 10$
OTH_MOR	Moose reported dead due to causes other than hunting (vehicle accidents, poaching, predation, etc.)	
Productivity indices		
CALV_FEM	Number of calves by 100 females in the harvest	$\frac{\text{calves harvested}}{\text{females} > 1.5 \text{ year old}} \times 100$
FEM_MILK	Females in lactation (%) in the harvest	$\frac{\text{females in lactation}}{\text{females} > 1.5 \text{ year old}} \times 100$
CA_RATIO	Sex ratio among calves in the harvest	$\frac{\text{male calves}}{\text{female calves}} \times 100$
Harvest rate indices		
PC_MALES	Proportion of males (%) among harvested adults	$\frac{\text{males} > 0.5 \text{ year old}}{\text{females} > 0.5 \text{ year old}} \times 100$
PC_YEAR	Proportion of 1.5 year-olds (%) in the harvest	$\frac{\text{yearlings}}{\text{moose} > 0.5 \text{ year old}} \times 100$
M_AGE	Mean age of adult males harvested	$\frac{\sum \text{age of males} > 0.5 \text{ year old}}{\text{males} > 0.5 \text{ year old of known age}}$
F_AGE	Mean age of adult females harvested	$\frac{\sum \text{age of females} > 0.5 \text{ year old}}{\text{females} > 0.5 \text{ year old of known age}}$
HUNTING CHARACTERISTICS		
LENGTH_D	Length (days) of the hunting season	
HD_10KM	Hunting pressure by all hunters / 10 km ²	$\frac{\text{hunting-days}}{\text{habitat area (km}^2\text{)}} \times 10$
HD_MOOSE	Hunting effort by moose harvested	$\frac{\text{hunting-days}}{\text{HARVEST}}$
LONGIT	Longitude at the centre point of the hunting zone	
LATIT	Latitude at the centre point of the hunting zone	

Table 1 continued...

VARIABLE	DEFINITION	DESCRIPTION
POPULATION CHARACTERISTICS		
WINT_POP	Total number of moose in the winter population after aerial survey	
COR_DENS	Density (moose / 10 km ²) corrected for visibility bias ¹	$\frac{\text{WIN_POP}}{\text{habitat area}} \times 10 \times \text{visibility}$
CA100F_W	Number of calves /100 females in winter population	$\frac{\text{calves observed}}{\text{females} \geq 1.5 \text{ year old}} \times 100$
%MALES_W	Percent males /in adult winter population	$\frac{\text{males} \geq 1.5 \text{ year old}}{\text{females} \geq 1.5 \text{ year old}}$
PRODUCT	% calves in autumn population	$\frac{\text{calves in winter} + \text{calv. harvested}}{\text{WIN_POP} + \text{HARVEST}}$
HAR RATE	Harvest rate (%): proportion of autumn population removed by hunting	$\frac{\text{HARVEST}}{\text{WIN_POP} + \text{HARVEST}}$
RATE_INC	Rate of increase	$\frac{100 - \text{HAR_RATE}}{100 - \text{PRODUCT}}$

¹Visibility = 0.73 (Crête *et al.* 1986), except for zones 1 and 2 where visibility = 0.52 (Courtois *et al.* 1991b)

precision of the predictions by computing the relative difference (%) between predicted and observed values.

Finally, a complete-link cluster analysis (Legendre and Legendre 1979) was used to associate moose populations of various hunting zones based on the biological characteristics of the harvest. Analyses involved 312 records corresponding to the hunting statistics published since 1973 (Gauthier and Roy 1981; Roy 1985; Breton 1991). Calculations were based on the Euclidean distance matrix calculated on standardized data to give an equivalent weight to each hunting statistic. The mean values for 1973-1984 and 1985-1990 were used because the zoning and its numbering system were changed in 1984. This approach makes it possible to compare the statistics for 1973-1984 to the recent situation.

RESULTS

Relations between hunting statistics and aerial surveys

Population parameters were correlated with hunting statistics. Moose density was related to moose harvest by surface area (Fig. 1), a simple regression explaining about 51% of the variation of moose density. Multiple linear regressions made it possible to improve predictions of the most important population parameters by using hunting statistics as independent variables (Table 2). Equations were the most precise for density ($R^2 = 0.74$) and harvest rate ($R^2 = 0.68$), intermediate for the percentage of adult males in winter, the number of calves/100 females and the rate of increase ($0.42 \geq R^2 \leq 0.52$), and the poorest for % calves in autumn ($R^2 = 0.23$). The equations generally involved 3 or 4 independent variables, but most of the variance (partial R^2) could be explained by 2 or 3 variables.

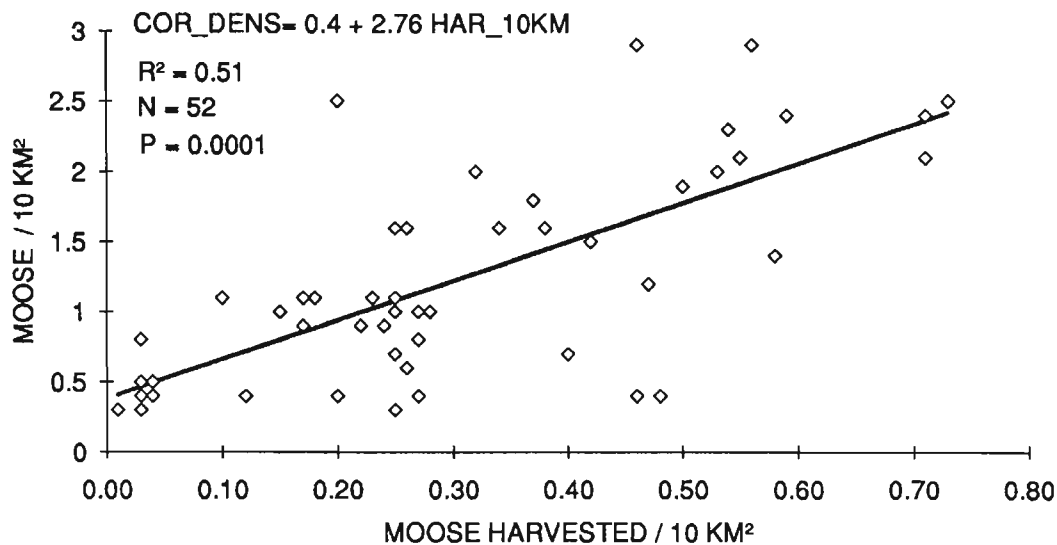


Fig. 1. Relation between corrected moose density (moose/10 km²) in winter (COR_DENS) and harvest/10 km² (REC_10KM) in the autumn preceding surveys.

Harvest per 10 km² explained an important part of the variance in models predicting density, harvest rate and rate of increase. Percentage of calves in autumn was explained exclusively by the percentage of lactating females in the harvest, while the number of calves/100 females in winter could be predicted mainly by the number of calves/100 females in the harvest. This latter variable also had a major influence when predicting harvest rate. The predicted parameters showed major regional variations, particularly along the east-west axis, as reflected by the high partial R² for longitude in most equations.

Cross-validation revealed that the models gave, on average, unbiased and relatively precise predictions (Table 3). Mean predicted values were very similar ($\leq 4\%$) to those observed for the 52 aerial surveys. Differences were often greater for a single prediction. Rate of increase and sex ratios were best predicted while the poorest model concerned cow:calf ratios which gave on average a $\pm 29\%$ precision. It seems relevant to mention that the median of differences was always lower than the mean indicating that few bad predictions tended to overestimate the prediction variability.

Regression models were used to reconstruct moose populations in hunting zones 3 and 15 (Fig. 2). These zones were chosen because they were known to exhibit two different trends. Recent aerial surveys and hunting statistics suggested that moose population was growing in the first one and declining in the second. Models supported these observations. They showed that moose density in zone 15 gradually increased between the early seventies and the mid-eighties but decreased thereafter until 1989. The current density is about 1.5 moose/10 km². The harvest rate and the % calves in autumn gradually increased while the rate of increase was negative during the eighties.

Moose density was lower in zone 3 (≈ 1.3 moose/10 km²). It grew by more than 50% between 1974 and 1983, followed by a major decline up until 1986. The situation improved thereafter, possibly due to greater productivity in the mid-eighties. Harvest rate of this population is very high (30-40%), and models predict an annual decline in the herd. The predicted decline seemed however less significant during the years the herd was growing.

Table 2. Multiple regression models predicting parameters of Québec moose populations from hunting statistics and geographical position (longitude, latitude) of management units. LN and SQRT mean naperian logarithmic and square root transformations of concerned variables. Other variable definitions are given in Table 1.

INDEPENDENT VARIABLES	PARAMETER VALUE	STANDARD ERROR	PARTIAL R ²	P
Winter density (COR_DENS: R ² = 0.74; DF = 49; F = 31.82; P = 0.0001)				
INTERCEPT	15.771	7.420	–	0.0391
HAR_10KM	1.657	0.385	0.49	0.0001
LONGIT	0.058	0.017	0.16	0.0012
CALVES_FEM	-0.010	0.003	0.04	0.0026
LN (LATIT)	-4.820	1.834	0.04	0.0117
Calves (%) in autumn (PRODUCT: R ² = 0.23; DF = 25; F = 7.06; P = 0.0138)				
INTERCEPT	6.269	6.003	–	0.3068
FEM_MILK	0.255	0.096	0.23	0.0138
Harvest rate (HAR_RATE: R ² = 0.68; DF = 49; F = 24.29; P = 0.0001)				
INTERCEPT	92.547	20.682	–	0.0001
SQRT (HAR_10KM)	36.686	5.182	0.24	0.0001
CALVES_FEM	0.145	0.052	0.25	0.0077
LONGIT	-1.169	0.267	0.17	0.0001
LN (F_ÂGE)	-10.244	5.957	0.02	0.0924
Rate of increase (RATE_INC; R ² = 0.52; DF = 25; F = 7.98; P = 0.0009)				
INTERCEPT	-0.502	0.527	–	0.3516
HAR_10KM	-0.508	0.153	0.16	0.0032
LN (F_ÂGE)	0.311	0.167	0.26	0.0764
LONGIT	0.017	0.008	0.10	0.0447
Percentage of adult males in winter (%MALES_W; R ² = 0.49; DF = 31; F = 8.89; P = 0.0003)				
INTERCEPT	337.726	79.242	–	0.0002
LN (LONGIT)	-74.305	18.045	0.24	0.0003
PC_MALES	0.366	0.132	0.20	0.0099
CALVES_FEM	-0.069	0.042	0.05	0.1012
Calves/100 females in winter (CA100F_W; R ² = 0.42; DF = 31; F = 6.86; P = 0.0013)				
INTERCEPT	62.424	72.080	–	0.3938
LN (CALVES_FEM)	16.808	8.324	0.30	0.0531
LONGIT	-1.421	0.741	0.07	0.0654
FEM_MILK	0.434	0.270	0.05	0.1087

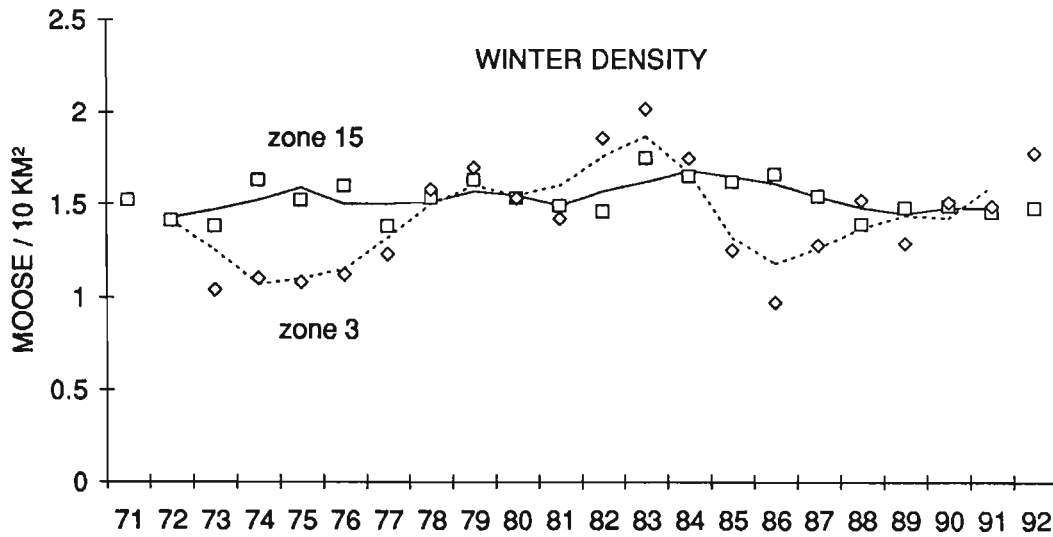


Fig. 2. Predicted biological characteristics of moose populations in hunting zones 3 and 15 based on the multiple regression models of Table 2. a) winter density;

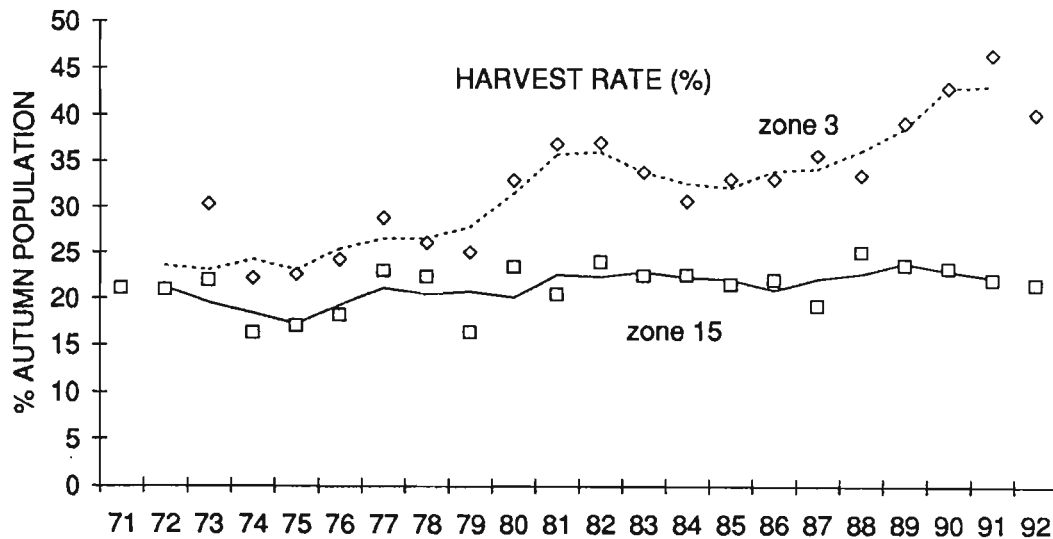


Fig. 2. Continued... b) harvest rate;

Specificity of hunting zones

Cluster analysis identified 5 interpretable groups of hunting zones under an Euclidean distance of 1.25 (Fig. 3). This limit distance was chosen because the groups became much less tight beyond that point. The analysis is interpretable on a geographical scale, with the neighbouring hunting zones generally tending to group together (Fig. 4).

The first group was made up of hunting zones located south of the St. Lawrence River

(current zones 1, 2, 3 and 4; Fig. 4b), to which zone 11 was also associated. The basic statistics show that this group was characterized by moderate harvest per surface area and high productivity (Table 4).

The second group (in north-central Québec) was the largest one. It combined hunting zones located between 48° and 50° latitude. This group included current zones 14, 16, 17 and 18 east. It was characterized by low yield, high proportion of males and a

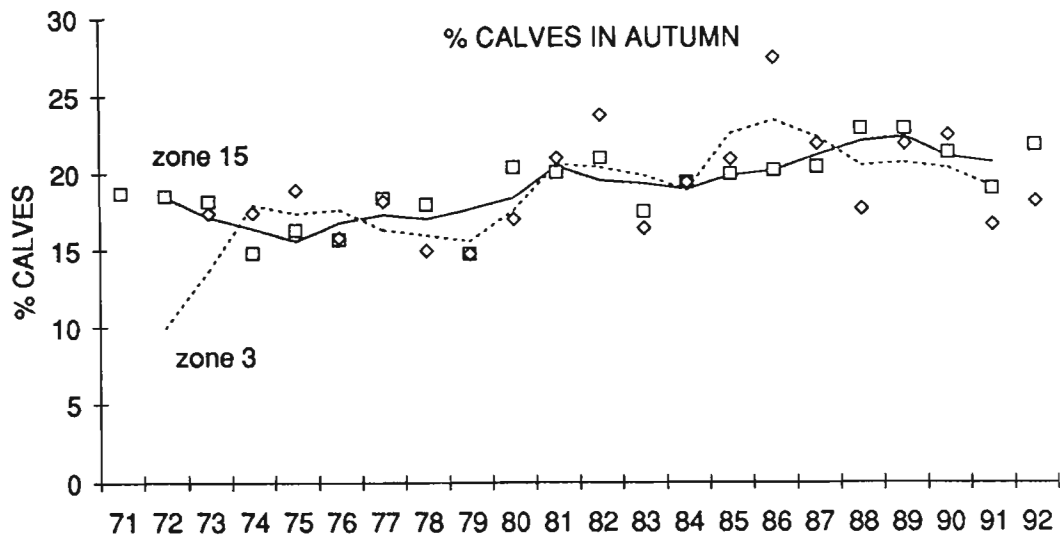


Fig. 2. Continued... c) % calves in autumn;

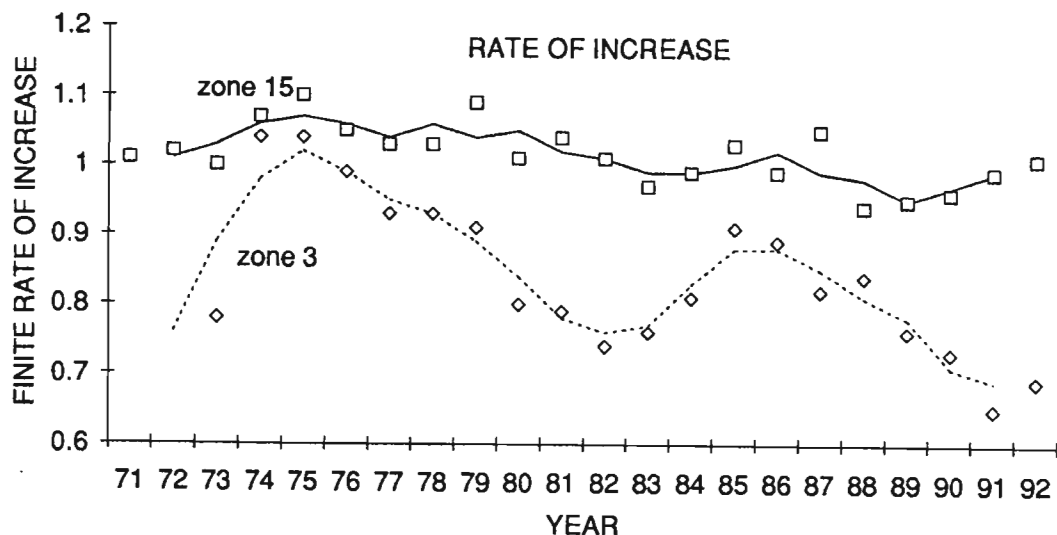


Fig. 2. Continued... d) finite rate of increase. Discrete points identify predicted values and lines represent their 3-point moving average.

fairly large number of calves and yearlings. Densities were low but sex ratio was near parity and productivity was high. This group of zones required the greatest number of hunting-days by moose harvested.

The third group included zones of western Québec (current zones 9, 10 and 12). This group was characterized by low productivity, high yield and high densities.

The fourth group was composed of zones located in central Québec (13, 15 and 18

west), to which zone 7 may also be added. This group possessed average characteristics for all variables studied, except for sex ratio among calves which was very low. This group also stood out due to high hunting pressure (hunting-days/10 km²).

The last interpretable group included the northern zones (19 and 22), which were mainly characterized by a very low yield, including few young animals and a high proportion of old males. Density and productivity were

Table 3. Evaluation, by cross-validation, of regression models computed to predict density and composition of moose populations. The observed parameters are those estimated in all aerial surveys ($24 < n < 52$).

	OBSERVED	PREDICTED	DIFFERENCE (%)	
	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	median
POPULATION CHARACTERISTICS IN WINTER				
Moose/10km ²	1.29 ± 0.10 ¹	1.30 ± 0.09	25.4 ± 3.6	16.1
Males/females (%)	34.8 ± 1.1	34.8 ± 0.6	13.1 ± 1.9	9.3
Calves/100 females	52.8 ± 3.1	52.7 ± 1.6	28.6 ± 4.9	24.6
POPULATION CHARACTERISTICS IN AUTUMN				
% calves	22.2 ± 1.0	21.3 ± 0.4	19.7 ± 4.3	13.1
Harvest rate (%)	20.7 ± 1.5	21.6 ± 1.2	26.6 ± 3.8	21.9
Rate of increase	1.019 ± 0.035	1.005 ± 0.017	9.0 ± 1.5	7.2

very low, and sex ratio among adults was almost balanced.

Zones 6 and O₂ were joined together but this group cannot be interpreted due to the small number of observations ($n < 9$). Similarly, zones 5, 8 and 20 were not associated with any other hunting zone. These zones correspond to sectors where moose were virtually absent (zones 5 and 8), or subject to very limited harvesting (zone 20).

DISCUSSION

Québec's system for monitoring moose populations is a reliable tool (Courtois 1989). Complexity is its main weakness: wildlife managers must annually examine several indices which sometimes show conflicting trends due to sampling imprecision and to annual variability of hunting conditions (Courtois and Lamontagne 1990). Each hunting zone has unique characteristics, so management should be done at this level. On the other hand, it is impossible to make a global judgment on the Québec herd by examining each hunting zone on its own due to the large amount of data that must be considered simultaneously. A good compromise would be to monitor

each zone separately as we presently do, but to apply the same hunting strategies to all similar zones, as detected with cluster analysis, since they exhibit similar population characteristics. This would give a limited number of strategies, thereby simplifying regulation for hunters.

The monitoring of populations can be substantially simplified through the use of multiple regression models. The latter permit the integration of several indices which reduces redundancy of data and greatly facilitates interpretation. We suggest calculation of only 4 indices to monitor moose populations: density (or total population), % calves in autumn, harvest rate and rate of increase. Trends shown by these 4 indices, calculated annually, with the help of the models would be sufficient to understand the dynamics of harvested moose populations.

The models are not biased judging by the 52 simulations done with cross-validation. However, single predictions are less precise (9-29%), but this precision appears acceptable as the aerial surveys themselves present a relative error of approximately 20% (Courtois 1991b). Moreover, it is likely that a

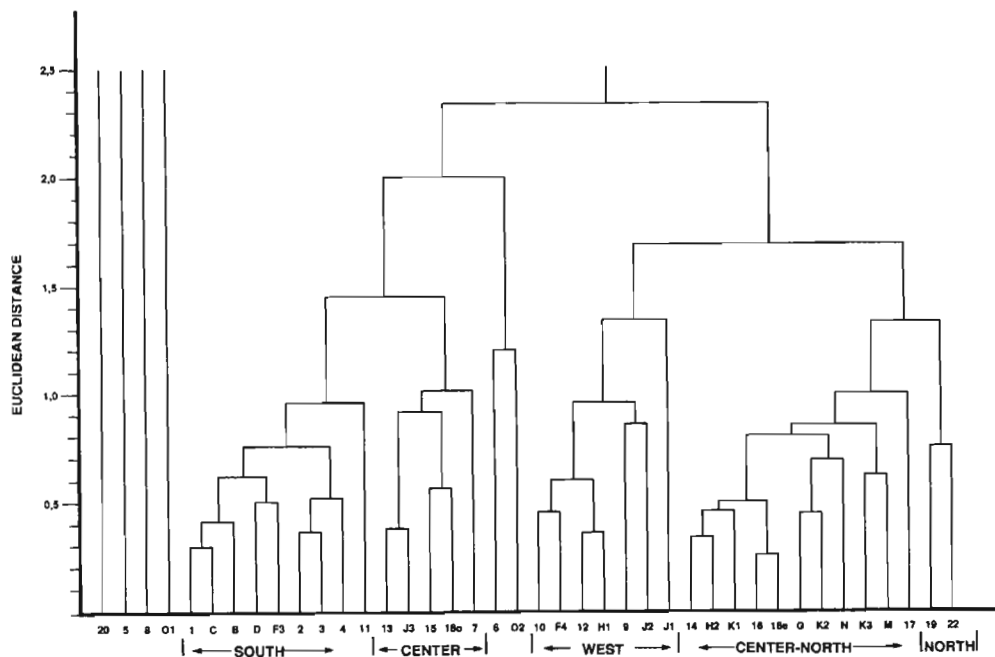


Fig. 3. Dendrogram (complete link) of Québec hunting zones according to characteristics of moose harvest.

significant part of the error is attributable to imprecise hunting statistics themselves due to variations in hunting conditions and inevitable sampling errors (Courtois 1989) despite standardized methods. In such a case, it would be preferable to use moving averages over a few years to smooth out the predicted values or the hunting statistics before applying the regression models. Nevertheless, one must examine predicted historical series at least 4-5 years long before being certain of population trends.

Density and harvest rate models are the most reliable ($R^2 \approx 0.70$) and they possess seemingly the widest predictive range because they are based on the largest sample size ($n \geq 50$). Special attention must be paid to the rate of increase. This indicator does not take into account natural mortalities and thus overestimates the real population rate of increase. However, natural mortality varies from one population to the next so there is no simple method to evaluate it. Natural mortalities fluctuate between 10 and 20% per year among

populations subject to high predation and between 4 and 11% when predation is lower (Fryxell *et al.* 1988). Natural mortality also varies according to moose density. In southwestern Québec, Messier and Crête (1985) calculated annual losses due to predation of 19.3% in those sectors where moose was abundant ($3.7/10 \text{ km}^2$) but only 6.1% with densities of $1.7 \text{ moose}/10 \text{ km}^2$. Major regional variations are also noted; radio-collared moose had a natural mortality rate of 9% on the North Shore of the St. Lawrence River (Courtois *et al.* 1993) and of 3-5% in Eastern Québec (R. Courtois, unpublished data). The rate of increase must therefore be interpreted in light of the biological characteristics prevailing in each hunting zone (density, predation, etc.). An estimate of the real rate of increase can however be obtained only by comparing the estimated autumn populations for successive years. Such an approach would provide results easier to interpret in the absence of other sources of information.

Regression models were developed on

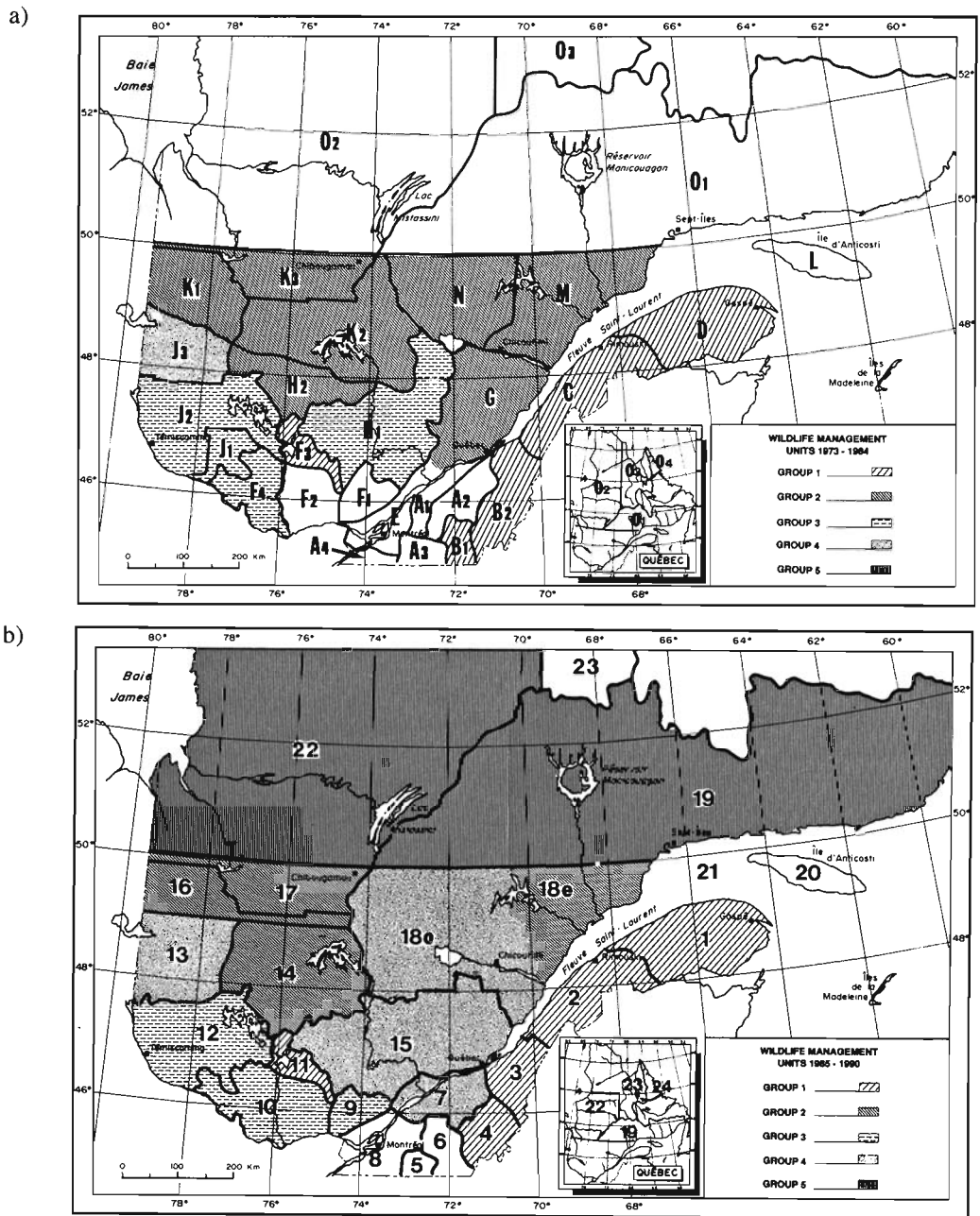


Fig. 4. Grouping of management units as defined by complete-link cluster analysis based on hunting statistics a) mean 1973-1984 and b) mean 1985-1990.

the basis of surveys carried out over the entire Québec territory. Several indices are influenced by the geographical scale as indicated by the partial determination coefficients: 16 to 24% of the variance in density, harvest rate and the % of males in winter were explained

by longitude. Cluster analysis also demonstrated that moose population characteristics depicted important regional differences. Knowing that, it should theoretically have been more logical and more precise to develop independent models for each group of

Table 4. Harvest, hunting and population characteristics ($\bar{x} \pm SE$) for the 5 most important groups of hunting zones identified using the cluster analysis. Variable definitions are given in table 1.

	GROUP 1 (SOUTH)	GROUP 2 (NORTH-CENTRE)	GROUP 3 (WEST)	GROUP 4 (CENTRE)	GROUP 5 (NORTH)
Harvest characteristics (9 < n < 96)					
HAR_10KM	0.3 ± 0.0	0.2 ± 0.0	0.5 ± 0.0	0.4 ± 0.0	< 0.1 ± 0.0
OTH_MOR	23 ± 2	16 ± 1	24 ± 3	62 ± 4	10 ± 2
CALV_FEM	83 ± 2	62 ± 2	46 ± 2	62 ± 2	39 ± 3
FEM_MILK	58 ± 1	61 ± 2	52 ± 1	59 ± 1	49 ± 3
CA_RATIO	117 ± 4	107 ± 8	120 ± 12	98 ± 5	114 ± 16
PC_MALES	55 ± 1	60 ± 1	56 ± 1	56 ± 1	62 ± 4
PC_YEAR	42.5 ± 0.8	39 ± 1	34 ± 1	39 ± 1	34 ± 3
M_AGE	2.8 ± 0.0	3.4 ± 0.1	3.5 ± 0.1	3.1 ± 0.1	4.2 ± 0.2
F_AGE	3.6 ± 0.1	4.1 ± 0.1	4.7 ± 0.1	4.2 ± 0.1	4.0 ± 0.2
Hunting characteristics (2 < n < 78)					
LENGTH_D	10 ± 0	23 ± 0	14 ± 1	18 ± 1	26 ± 2
HD_10KM	27 ± 3	16 ± 2	27 ± 2	42 ± 4	2 ± 1
HD_MOOSE	88 ± 6	100 ± 8	61 ± 5	87 ± 13	83 ± 12
LONGIT	70.5 ± 0.4	74.1 ± 0.4	76.8 ± 0.2	74.9 ± 0.5	71.0 ± 0.9
LATIT	47.3 ± 0.2	49.2 ± 0.1	46.6 ± 0.1	48.0 ± 0.2	51.9 ± 1.1
Population characteristics (2 < n < 17)					
WINT_POP	804 ± 138	2 174 ± 278	2 716 ± 401	4 123 ± 749	6 588 ± 1 221
COR_DENS	0.8 ± 0.1	0.9 ± 0.1	2.1 ± 0.1	1.8 ± 0.3	0.4 ± 0.1
CA100F_W	68 ± 6	57 ± 5	34 ± 6	54 ± 6	41 ± 1
% MALES_W	32 ± 4	36 ± 2	31 ± 2	32 ± 2	48 ± 1
PRODUCT	24 ± 2	24 ± 3	18 ± 2	23 ± 1	17 ± 1
HAR_RATE	33 ± 4	16 ± 1	20 ± 1	21 ± 1	5 ± 4
RATE_INC	0.85 ± 0.09	1.15 ± 0.07	1.00 ± 0.03	1.04 ± 0.03	1.15 ± 0.04

hunting zones identified by cluster analysis. However, this approach was not possible because we had insufficient data to compute models for some groups. Because we wanted few models valid for all the province, we tried to take into account the regional variations in biological parameters through the inclusion of longitude and latitude in the models. This method seems acceptable considering the limits of our data set. In the actual context, it was necessary to do so in order to maximise the precision of the predicted values, as up to 24% of the variance could be explained by these variables.

Several indices were highly correlated to the harvest/10 km². This variable explains 49% of the variance of predicted density. It means that every independent factor liable to increase the harvest, such as an increase in hunting pressure or improved access, would lead to an apparent increase in predicted density. This can limit reliability of models for the description of temporal changes over long periods in hunting zones where the hunting pressure changed. Predictive models would be more accurate if they took into account hunting pressure, but mail surveys were not frequent enough or precise enough for this

variable to be useable in our models. In most hunting zones in Québec, densities are lower than the one allowing maximum sustained yield, on the left side of the bell-shape density/harvest curve (Crête 1987). For this reason, increase in harvest parallels increasing density. However, for jurisdictions with conservative quotas and populations close to carrying capacity, the relationship between harvest and density would be negative.

It is important to point out that the predicted harvest rate for hunting zone 3 seemed over-estimated, whereas the rate of increase appeared under-estimated. The latter indicator even suggested a decline in density during the entire period under study whereas, judging from harvest and vehicle collision, the population grew between 1974 and 1983 as well as after 1986. However, trends predicted by the models conformed to those noted at the time of the aerial surveys. Aerial censuses indicated harvest rates greater than 30% and density declines, while the harvest remains very high. This situation, which prevails in all hunting zones south of the St. Lawrence River, can be attributed to an influx of moose from neighbouring territories. While the actual extent of this phenomenon has never been quantified, Desrosiers *et al.* (1989) showed, for example, that 50% of the harvest of hunting zone 1 was taken less than 15 km from the park and wildlife reserves located in the centre of the zone.

The predictive models that we computed would probably suffice for managing moose in Québec without costly aerial surveys if hunting pressure and regulations remained the same in the future. However, selective hunting will be introduced in 1994 in most hunting zones. For this reason, it will be necessary, before dropping aerial censuses, to compute new regression models based on the male segment of the population for which no selective harvest will apply.

ACKNOWLEDGMENTS

The authors would like to thank Yves Leblanc and Jean Maltais for their cooperation in preparing a preliminary report. They are also indebted to Claude Dussault, André Gingras, Jean Tremblay and two anonymous reviewers who kindly commented on a previous draft, as well as to Jean Berthiaume for preparing the figures and to Christiane Picard for typing the text.

REFERENCES

- BERGERUD, A.T. and J.P. ELLIOT. 1986. Dynamics of caribou and wolves in northern British Columbia. *Can. J. Zool.* 64: 1515-1529.
- BOUCHARD, R. 1990. Gros gibier au Québec en 1989 (exploitation par la chasse et mortalité par des causes diverses). Québec, Min. Loisir Chasse et Pêche, Dir. gestion espèces habitats, 50 p. SP 1760-08-90.
- BRETON, L. (éd.). 1991. Compte rendu du neuvième atelier sur la grande faune tenu à Québec du 29 avril au 2 mai 1991. Québec, Min. Loisir Chasse et Pêche, Dir. gestion espèces habitats, 351 p. SP 1906-08-91
- CAUGHLEY, G. 1974. Productivity, offtake and rate of increase. *J. Wildl. Manage.* 38:566-567.
- COURTOIS, R. 1989. Analyse du système de suivi de l'Orignal au Québec. Québec, Min. Loisir Chasse et Pêche, Dir. gestion espèces habitats, 48 p. SP 1770-09-90.
- . 1991a. Normes régissant les travaux d'inventaires aériens de l'orignal. Québec, Min. Loisir Chasse et Pêche, Dir. gestion espèces habitats, 24 p. SP 1907-08-91.
- . 1991b. Résultats du premier plan quinquennal d'inventaire aériens de l'orignal au Québec, 1987-1991. Québec, Min. Loisir Chasse et Pêche, Dir. gestion espèces habitats, 36 p. SP 1921-12-91
- , M. CRÊTE and F. BARNARD. 1993. Productivité de l'habitat et

- dynamique d'une population d'orignaux du sud de la taiga québécoise. Québec, Min. Loisir Chasse et Pêche, Dir. faune et habitats et Dir. rég. Côte-Nord, 51 p. SP 2144-08-93
- _____ and G. LAMONTAGNE (éd.). 1990. Diagnostic sur l'état des populations d'orignaux au Québec. Québec, Min. Loisir Chasse et Pêche, Serv. faune terr. et Serv. aménage. expl. faune, 37 p. SP 1785-04-91.
- CRÊTE, M. 1987. The impact of sport hunting on north american moose. Swedish Wildl. Res. Suppl. 1: 553-563.
- _____ and C. DUSSAULT. 1986. Interprétation des statistiques de chasse de l'orignal. Québec, Min. Loisir Chasse et Pêche, Dir. faune terr., 27 p. SP 1036-03-86.
- _____ and F. GOUDREAU. 1980. Les bois, la tache vulvaire et la couleur du museau pour déterminer le sexe des orignaux (*Alces alces americana*) en janvier dans le sud-ouest du Québec. Proc. N. Am. Moose Conf. Workshop 16:275-288.
- _____, L.-P. RIVEST, H. JOLICOEUR, J.-M. BRASSARD and F. MESSIER. 1986. Predicting and correcting helicopter counts of moose with observations made from fixed-wing aircraft in southern Québec. J. Appl. Ecol. 23:751-761.
- DESROSIERS, A., M. FORTIN, A. PELLETIER, J.-M. PARISÉ and R. COURTOIS. 1989. Inventaire aérien de l'orignal dans la zone de chasse 1 en janvier 1987. Québec, Min. Loisir Chasse et Pêche, Dir. rég. Bas-Saint-Laurent/Gaspésie/Îles-de-la-Madeleine, et Dir. gestion espèces habitats, 43 p. SP 1573-10-89.
- FRYXELL, J.M., W.E. MERCER and R.B. GELLATELY. 1988. Population dynamics of Newfoundland moose using cohort analysis. J. Wildl. Manage. 52:14-21.
- GASAWAY, W.C. and S.D. DUBOIS. 1987. Estimating moose population parameters. Swedish Wildl. Res. Suppl. 1:603-617.
- GAUTHIER, C. and M.-H. ROY. 1981. Répertoire de données sur les zones de chasse et les populations d'orignaux (1971 et 1980). Québec, Min. Loisir Chasse et Pêche, Dir. rech. faune. 6 p. + annexes.
- IQOP. 1985. Étude sur la chasse récréative au gros gibier en 1984 par les résidents du Québec. Institut québécois d'opinion public, et Québec, Min. Loisir Chasse et Pêche, Dir. gén. faune, 71 p. SP 1024-11-85.
- LACASSE, M. and J. PELLETIER. 1979. Aspects socio-économiques de l'exploitation de l'orignal par la chasse sportive au Québec en 1978. Québec, Min. Loisir Chasse et Pêche, Serv. rech. socio-écono. 73 p.
- LEGENDRE, L. and P. LEGENDRE. 1979. Écologie numérique. Vol. 2. La structure des données écologiques. Masson, Paris et Les Presses de l'Université du Québec, Montréal, 254 p.
- MESSIER, F. and M. CRÊTE. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia 65:503-512.
- NEDELCA, S. 1991. Rapport de l'enquête sur la chasse de l'orignal, saison 1990. Bureau de la statistique du Québec, Dir. Méthodologie, rapport préliminaire non paginé.
- PELLETIER, J. and G. THERRIEN. 1977. La chasse sportive à l'orignal au Québec en 1973-1974 et en 1976-1977. Édition corrigée et résultats complémentaires. Québec, Min. Tour. Chasse et Pêche, Dir. planif., serv. rech. socio-écono., 110 p.
- _____ and G. THERRIEN. 1978. La chasse sportive à l'orignal au Québec en 1976. Québec, Min. Tour. Chasse et Pêche, Dir. Planif., serv. rech. socio-écono., 57 p.
- RIVEST, L.-P., H. CRÉPEAU and M. CRÊTE. 1990. A two phase sampling plan for the estimation of the size of a

- moose population. *Biometrics* 46:163-176.
- ROY, M.-H. 1985. *Statistiques de la chasse à l'original*. Québec, Min. Loisir Chasse et Pêche, Dir. faune terr., doc. travail.
- SAS INSTITUTE. 1987. *SAS/STAT guide for personal computers, version 6 edition*. SAS Institute inc., Cary, NC, USA, 1028 p.
- SNEDECOR, G.W. and W.G. COCHRAN. 1971. *Méthodes statistiques, 6^e édition*. Association de coordination technique agricole, Paris, 649 p.
- STATBEC. 1984. *La chasse récréative au Québec en 1981*. Min. Loisir Chasse et Pêche, Dir. gén. faune, 170 p.
- TIMMERMANN, H.R. 1974. Moose inventory methods: a review. *Naturaliste can.* 101:615-629.