# THE USE OF SCHAEFER'S AND FOX'S SURPLUS-YIELD MODELS TO ESTIMATE OPTIMAL MOOSE HARVEST AND HUNTING EFFORT

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ABSTRACT: We studied changes in moose harvest-per-unit of effort (CUE) in Québec wildlife reserves to estimate maximum sustainable yield. Using data from the beginning of controlled moose hunts in 1962, we examined 5 parameters used to express the hunting effort. Since all 5 were significantly correlated with each other ($P < 0.01$), we selected the simplest and most intuitive one, number of hunting-days, to calculate surplus-yield models. Hunting effort, expressed as the number of hunting-days, grew exponentially over the last 30 years, but harvest did not, resulting in a progressive decline in CUE. Among the 6 biological indices used to manage moose populations in wildlife reserves, only the yearling (1.5 year) percentage, which had risen gradually from 1962, seemed sensitive to harvest rate modifications. Both Schaefer's and Fox's surplus-yield models produced significant equations thus permitting the application of surplus-yield models. Hunting effort explained 60% of CUE variances in 8 of the 10 wildlife reserves where sufficient data were available. Schaefer's and Fox's models were also tested in zecs (controlled harvest zones), territories managed by hunter's associations since the late seventies, using hunting effort parameters. Explained variance ($0.36 < r^2 < 0.74$) was generally lower in zecs than in wildlife reserves probably because hunting effort was not recorded as precisely in zecs as in wildlife reserves. Models applied to reserves suggest maintaining harvest at around 0.45 moose/10 km$^2$ in the central part of Québec. In eastern Québec, south of the St. Lawrence River, moose populations can sustain a greater harvest (0.5-0.9 moose/10 km$^2$) probably due to a very low predation rate. Where predation is present and in northern parts of the province, the harvest must be less than 0.3 moose/10 km$^2$. Models suggest maintaining effort between 3 and 19 hunting-days/10 km$^2$ depending on the reserve. Optimal harvest and effort given by the models are generally greater in zecs than in reserves.

RÉSUMÉ: Nous avons étudié les changements du nombre de captures par unité d'effort (CUE) afin d'estimer la récolte maximale soutenue de l'orignal dans les réserves fauniques du Québec. Comme les 5 indices d'effort de chasse examinés étaient fortement corrélés ($P < 0.01$), nous avons retenu le plus intuitif et le plus simple, le nombre de jours de chasse, pour calculer les modèles de rendement globaux. L'effort de chasse a augmenté exponentiellement au cours des 30 dernières années alors que la récolte a progressé beaucoup plus lentement ce qui a amené une diminution progressive des CUE, permettant ainsi l'application des modèles de rendement globaux. Parmi les 6 indicateurs biologiques utilisés pour le suivi des populations, seul le % d'animaux de 1.5 an, qui a augmenté de façon graduelle, a paru sensible aux changements du niveau d'exploitation. Les modèles de rendement globaux de Schaefer et de Fox s'ajustent bien aux données des réserves fauniques, l'effort de chasse expliquant 60 % de la variance des CUE dans 8 des 10 réserves fauniques où des données suffisantes étaient disponibles. Les modèles de rendement globaux ont également été appliqués avec succès dans les zecs (zones d'exploitation contrôlées) du centre du Québec. La variance expliquée ($0.36 < r^2 < 0.74$) était cependant moins élevé probablement parce que l'effort de chasse y est mesuré avec moins de précision. Les modèles appliqués aux réserves suggèrent de maintenir la récolte autour de 0.45 orignal/10 km$^2$ dans le centre du Québec. Dans l'est, au sud du fleuve Saint-Laurent, les populations d'orignaux pourraient soutenir une récolte plus élevée (0.5-0.9 orignal/10 km$^2$) probablement à cause d'une prédation moins grande. Là où la prédation existe et dans la partie nord de la province, la récolte devrait être inférieure à 0.3 orignal/10 km$^2$. Les modèles suggèrent de maintenir un effort de 3 à 19 jours de chasse/10 km$^2$ selon la réserve considérée. La récolte et l'effort optimaux sont généralement plus grands dans les zecs que dans les réserves.

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The province of Québec was divided into 25 fishing, hunting and trapping zones in order to manage wildlife populations. Two kinds of territories can be found in each zone: 1) free-access lands where everyone can hunt provided that they have a hunting licence; and 2) structured territories where hunters must pay an access fee to hunt. The most important structured territories are wildlife reserves (Fig. 1), public lands managed directly by the Québec government where hunting is strictly controlled through a limited number of licences, and zecs where access is loosely controlled by hunters associations. Other territories include outfitting areas, where access is controlled by private firms and parks, where hunting is prohibited.

Moose is the game species most coveted by Québec hunters. Each year, about 150,000 hunting licences are sold for that species. However, this activity is quite recent since there was less than 10,000 moose hunters in the mid-fifties (Courtois and Lamontagne 1990). Moose hunting made it possible to satisfy a growing demand for outdoor activities. The beginning of moose hunting in reserves in 1962, the abolition of the moose buck law two years later, the decline in white-tailed deer (*Odocoileus virginianus*) during the sixties and the seventies, and the abolition of the private hunting and fishing clubs to create zecs in 1978 providing access to good hunting territories were the most important incentives for this activity (Courtois and Lamontagne 1991).

At the present time, more than 5,500 hunters have access to 24,000 km$^2$ of exclusive territories in Québec wildlife reserves, which produce a harvest of about 700 moose per year. In most reserves, hunting success (moose/100 hunters) is good, being 2-3 times greater than on adjacent free-access lands (provincial mean = 7 moose / 100 hunters; Courtois and Lamontagne 1990). In 1989, hunting effort, expressed as the number of hunting-days for all hunters, was 23 times greater than in 1962 (19,358 vs 851 hunting-days) due to 1) a gradual extension of the number of reserves offering this activity, 2) an increase in the hunting areas in most reserves and 3) a greater number of hunters. Harvest growth (127 to 746 moose from 1962 to 1989) was less inportant, resulting in a gradual decline in the hunting success (1962: 42 moose

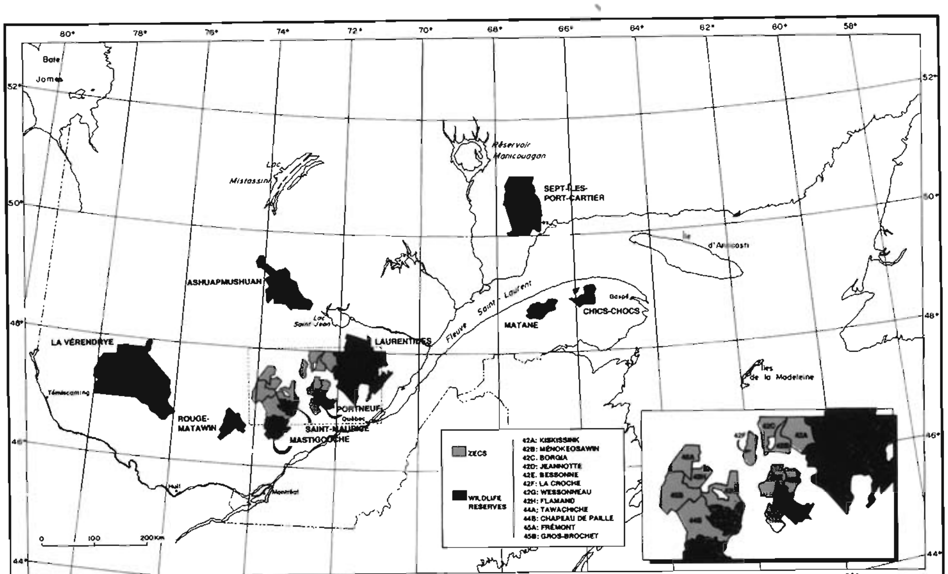

Fig. 1. Location of Québec wildlife reserves supporting moose populations.

/ 100 hunters; 1989: 14 moose / 100 hunters) and the harvest per unit of effort.

In 1978, 62 zecs were created in Québec. Currently, they cover close to 48,000 km$^2$ where about 27,000 moose hunters hunt each year with a mean success of about 7%. In these territories, moose harvest developed more rapidly than in reserves: with 1,134 moose harvested in 1978, the harvest reached about 1,800 moose in 1982 but tended to decline thereafter. Hunting effort peaked (198,534 hunting-days) in 1978 and has tended to stabilize at about 160,500 hunting-days in recent years.

Because historical data for reserves and zecs show that growth in the number of hunting-days over the last decades has led to a decline in the number of moose/hunting-days, we hypothesized that this relation is indicative of population changes. In such a case, maximum sustainable yield (MSY) and optimal number of hunting-days in structured territories could be estimated adequately by surplus-yield models such as those proposed by Schaefer (1954) and Fox (1970) for fish populations.

Under reasonably stable natural conditions, the net increase of an unharvested population is zero, at least on the average, as recruitment is balanced by natural deaths (Ricker 1975). At near maximum density, efficiency of reproduction is reduced through food competition, social stress, interactions between species or because the population contains older, less productive individuals. In populations limited by food, introducing harvesting lowers population abundance, increases population productivity through reduced competition, and thus creates a surplus which can be harvested. A similar mechanism could act in systems regulated by predators: reducing density will diminish predation because of increased searching time for predators thus improving recruitment. Surplus models postulate that populations produce their greatest harvestable surplus when they are at an intermediate level of abundance (Ricker 1975; Caughley 1976; Crête 1987). However, the relationship between harvest and effort is not linear: in response to a growing effort, harvest grows rapidly initially but tends to form a plateau, called the equilibrium yield, and declines thereafter if hunting effort continues to grow. In such a situation, the population becomes too small to support the harvest level. In this paper we discuss the applicability of these models to predict the optimal moose harvest and hunting effort in territories that could be compared to the Québec wildlife reserves and zecs. We also discuss the applicability of these models in both ecosystems regulated by food or predators.

## METHODS

Moose harvest and hunting effort were recorded at the check-points by interviewing hunters at the end of their hunting trips. For reserves, recent harvest data (1984-1989) were taken from annual publications of the Ministère du Loisir, de la Chasse et de la Pêche (Bouchard 1990; Breton 1990; Roy 1984a,b) while previous data were computed from information on file. Zec harvest and hunting effort data were provided by regional personnel (J. Archambault, Min. Loisir Chasse Pêche, pers. comm.). No selective harvest was in force during the period under study: hunters could harvest a male, a female or a calf.

The term "hunting effort" is often employed to represent the number of hunting-days necessary to kill a moose. In our paper, this term will be used in its general meaning and will designate total hunting capacity engaged during a specified period of time (Daget and LeGuen 1975; Ricker 1975). We used the year (hunting season) as the time period. We examined 5 hunting effort indicators (number of hunting parties, hunters, hunting-days, hunting-days/10 km$^2$, hunting-days/10 km$^2$ . day). To find the most sensitive indicator we made correlation analysis (Pearson's r) among them from the 3 wildlife reserves (Laurentides, La Vérendrye, and Matane) that had the longest historical series of data. Harvest characteristics such as number of moose harvested, moose harvest/10 km$^2$, moose harvested/100 hunters, hunting-days/moose, and biological indices computed from kill (% males, % yearlings, calves/100 females, % females in lactation and mean age of adult males and females) were also correlated with time to find which ones were the best indicators of population changes, assuming a gradual change paralleling harvest growth.

Schaefer's and Fox's surplus-yield models were tested using data from 10 reserves and 12 zecs where moose hunting data are available for 5 to 28 years. Schaefer's model (Schaefer 1954) postulates an inverse linear relationship between harvest (Y) and harvest/unit of effort (CUE). In this model, the relationship between harvest and effort (f) takes the form of a parabola: when effort increases, harvest increases up to a maximum called MSY and then sharply declines if effort continues to increase.

The parabolic equation for Schaefer's model is:

$$Y = af - bf^2 \qquad (1)$$

where a and b are the coefficients of the equation. This equation can be transformed as:

$$Y = f\,(a - bf)$$

and solved for Y=0:

$$0 = f\,(a - bf)$$

Two solutions are possible:

$$0 = f$$

which corresponds to the origin of the X,Y axis where there is no hunting. The second solution is:

$$0 = a - bf \qquad (2)$$

after transformation we obtain:

$$-a / -b = f$$

or

$$f = a/b \qquad (3)$$

This solution corresponds to the second parabola's intercept with the X axis and is the effort ($f_{max}$) necessary to eliminate the population. As the basic equation is a parabola, the optimum effort giving MSY corresponds to $f_{max}/2$, as a parabola is symmetric. Then, substituting in equation (3), we can find:

$$f_{opt} = a/2b \qquad (4)$$

MSY can be found by substituting $f_{opt}$ in equation (1):

$$MSY = af_{opt} - bf^2_{opt}$$

substituting $f_{opt}$ from (4),

$$MSY = a(a/2b) - b(a/2b)^2$$

$$MSY = a^2/2b - ba^2/4b^2 = 2a^2/4b - a^2/4b$$

$$MSY = a^2/4b \qquad (5)$$

The values of a and b can be found by computing harvest by unit of effort (CUE = harvest / effort) for each year where harvest and effort are known, and using regression analysis (CUE against f) knowing that the relation between CUE and f is linear:

$$CUE = a - bf \qquad (6)$$

Maximum number of moose that can be harvested (MSY) and optimal hunting effort ($f_{opt}$) giving MSY are computed substituting, in equation (5) and (4), numeric values for a and b found with regression analysis.

Fox's model (Fox 1970), on the other hand, stipulates that the relationship between CUE and f is curvilinear so CUE forms an asymptote to f, and harvest declines smoothly beside MSY. In Fox's model the relation between CUE and f can be simplified as:

$$\ln^{CUE} = a - bf \qquad (7)$$

CUE is found exponentiating the two parts of the equation:

$$CUE = e^{a-bf}$$

$$CUE = e^a\, e^{-bf} \qquad (8)$$

We find harvest by multiplying CUE by f,

$$Y = f\, e^a\, e^{-bf} \qquad (9)$$

According to Fox (1970), the optimum hunting effort is found by differentiating equation 9 with respect to effort and setting the result equal to 0,

$$dY / df = -b\, f\, e^a\, e^{-bf} + e^a\, e^{-bf} = 0$$

$$b\, f_{opt}\, e^a\, e^{-bf_{opt}} = e^a\, e^{-bf_{opt}}$$

After simplification, we find,

$$f_{opt} = 1/b \quad (10)$$

MSY is obtained for $f_{opt}$, after (9),

$$MSY = f_{opt}\, e^a\, e^{-bfopt}$$

Substituting $f_{opt}$ by its value in (10),

$$MSY = (1/b)\, e^a\, e^{-b/b} = (1/b)\, e^a\, e^{-1}$$

$$MSY = e^a / be \quad (11)$$

In this model, numeric values for a and b are also found with regression analysis ($\ln^{CUE}$ against f) after transforming CUE to its natural logarithmic form.

Schaefer's and Fox's basic equations can be summarized as follows:

| Model | Yield curve | Equilibrium curve | MSY | $f_{opt}$ |
|---|---|---|---|---|
| Schaefer | $Y = af + bf^2$ | $CUE = a - bf$ | $a^2/4b$ | a/2b |
| Fox | $Y = f\, e^a\, e^{-bf}$ | $\ln^{CUE} = a - bf$ | $e^a/be$ | 1/b |

As equilibrium curves have a negative slope, MSY and $f_{opt}$ computations are made using the absolute value for b. Computations were made using the SAS statistical package (SAS Institute 1987).

## RESULTS

Of the 5 hunting effort indicators computed, all were highly significantly correlated to each other (Table 1) but the number of hunting parties, the number of hunters and the number of hunting-days were more closely related to each other. The latter 2 hunting effort indicators also showed a steady growth from the first moose seasons in Laurentides, La Vérendrye and Matane reserves (Table 2). For these reasons we chose to use these 2 indicators in the surplus-yield models.

Correlations between time and harvest characteristics coming from these 3 reserves hunted for the longest period indicate that moose populations react differently in response to the progressive growth in the hunting effort. Harvest grew in Laurentides reserve, but declined in La Vérendrye reserve and remained stable in Matane (Table 2). But when the harvest is calculated on a standardized hunting effort unit, for example the number of moose harvested/100 hunters, then the strong inverse correlations suggest that the growth of the hunting effort has led to negative moose population changes (Table 2), although the relative importance of that change cannot be estimated.

These suspected moose population changes in the 3 older reserves were only correctly detected by the % of yearlings in Laurentides and La Vérendrye reserves (Table 2) although this biological indice change could also be interpreted as an increased recruitment or a lower level of hunter selection as older moose became less frequent. The weak % of male growth in the Matane reserve harvest during the period under study suggests a lowering of harvest rate which contra-

Table 1.Correlations (Pearson's r) between five hunting effort indicators in Québec wildlife reserves, 1962 - 1989. The effect of hunted area removed by partial correlation. n = 171.

| | No of hunting parties | No of hunters | No of H-D | Pressure | Debit |
|---|---|---|---|---|---|
| Number of hunting parties | -- | | | | |
| Number of hunters | 0.79** | -- | | | |
| Number of hunting-days (H-D) | 0.59** | 0.88** | -- | | |
| Pressure (H-D/10 km²) | 0.41** | 0.53** | 0.73** | -- | |
| Debit (H-D/10 km² . day) | 0.33** | 0.47** | 0.70** | 0.96** | -- |

** $P \leq 0.01$

Table 2.Correlation (Pearson's r) between year and hunting effort indicators, harvest characteristics and biological indices of the harvest in the three reserves hunted over the longest period.

| | LAURENTIDES[1] $11 \leq n \leq 28$ | LA VÉRENDRYE[2] $12 \leq n \leq 26$ | MATANE[2] $18 \leq n \leq 26$ |
|---|---|---|---|
| **HUNTING EFFORT INDICATORS** | | | |
| No of hunting parties | 0.93** | 0.90** | 0.00 |
| No of hunters | 0.94** | 0.90** | 0.69** |
| No of hunting-days (H-D) | 0.92** | 0.93** | 0.63** |
| Pressure (H-D/10 km2) | 0.92** | 0.61** | 0.46* |
| Debit (H-D/10 $km^2$ . day ) | 0.92** | 0.52* | 0.58* |
| **HUNTING STATISTICS** | | | |
| **1) Harvest characteristics** | | | |
| Moose harvested | 0.51** | -0.63** | -0.02 |
| Moose harvested/10 km2 | 0.56** | -0.88** | -0.43* |
| Success (moose/100 hunters) | -0.97** | -0.94** | -0.97** |
| H-D/moose | 0.92** | 0.92** | 0.82** |
| **2) Biological indices from kill** | | | |
| Adult males % | 0.20 | 0.36 | 0.38* |
| Yearlings % | 0.40* | 0.62** | 0.28 |
| Calves/100 females | -0.31 | -0.13 | 0.28 |
| Females in lactation (%) | 0.22 | -0.16 | 0.17 |
| Mean age of males | 0.03 | -0.41 | -0.16 |
| Mean age of females | 0.34 | 0.31 | -0.02 |

[1] Years 1962-1989
[2] Years 1964-1989

* $0.01 \leq P$ 0.05
** $P \leq 0.01$

dicts changes in the number of moose/100 hunters and the number of hunting-days/moose.

A gross approximation of the Québec wildlife reserve potential can be obtained by applying surplus-yield models to annual data for all reserves combined. In this particular case, both Schaefer's and Fox's models are highly significant (P = 0.0001) but Fox's model was the better suited ($r^2 = 0.93$ versus $r^2 = 0.87$). Using the number of hunters as a suitable indicator of hunting effort, this model suggests that all reserves combined can sustain a harvest of 647 moose with an optimal effort of 4,115 hunters per year. Very close results are obtained using the number of hunting-days as an indicator of hunting effort. In this case, Fox's model still gives the greater $r^2$ (0.93 versus 0.83). This model suggests a MSY of 667 moose per year; this harvest would be obtained with 10,667 hunting-days per year. Taking into account the hunted area, MSY could be estimated at 0.25 moose/10 $km^2$ for an optimum effort of 4 hunting-days/10 $km^2$ (Table 3).

The best way to estimate MSY and optimum effort is to apply the models to each reserve individually as in figures 2a and 2b. In

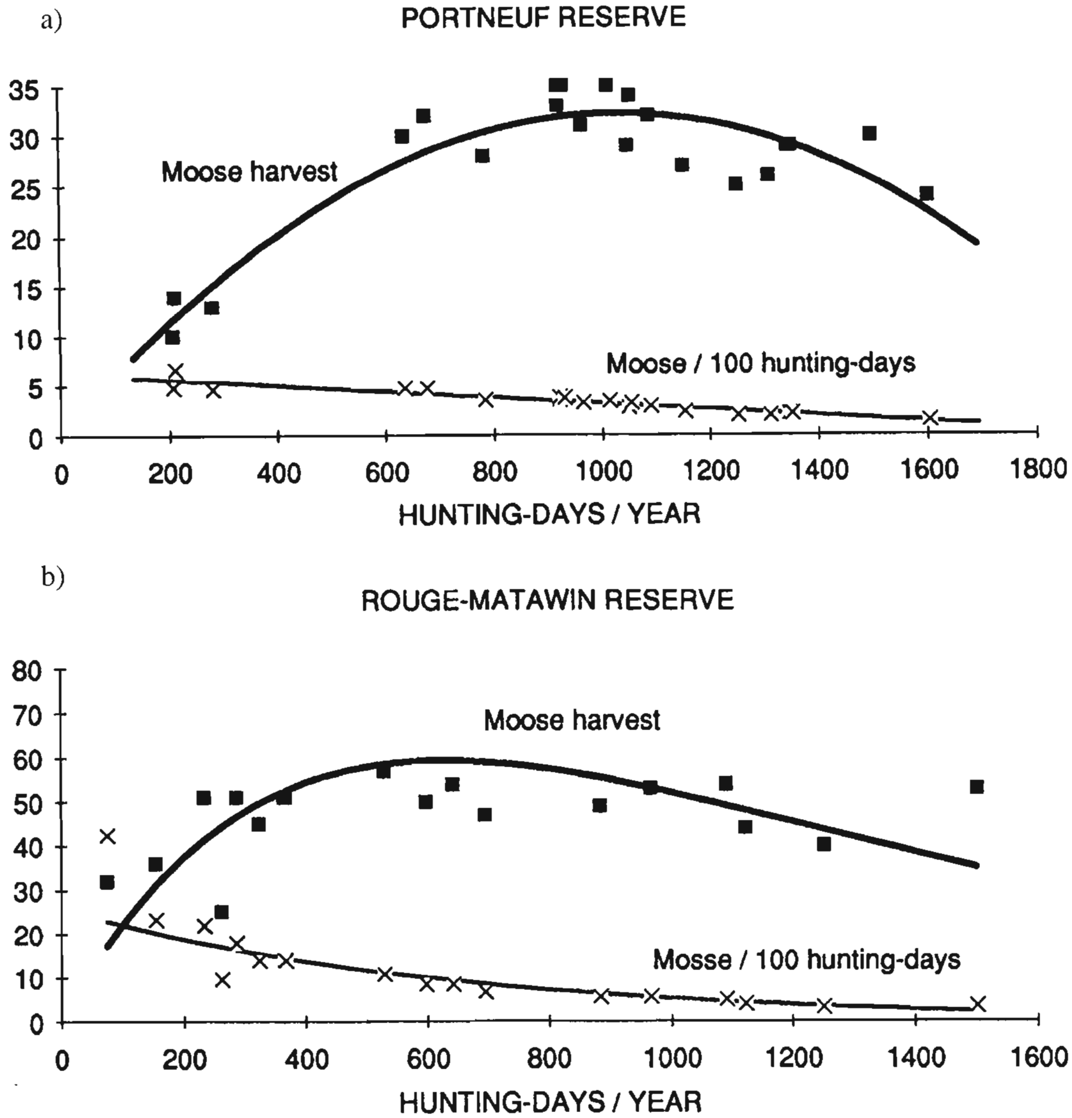


Fig. 2. Relationship between moose harvest and CUE (moose/100 hunting-days) (Y-axis) on the one hand and number of hunting-days (X-axis) on the other. a) Schaefer model applied to the Portneuf reserve data; b) Fox model fitted to the Rouge-Matawin reserve data. Yield curves (harvest) are computed using regression analysis coefficients from equilibrium (CUE) curves.

such a case, the relation between harvest per unit of effort and hunting effort is highly significant ($P = 0.0001$) in eight of the 10 reserves where hunting was allowed for $\geq 5$ years. Schaefer's and Fox's models give similar results and both models can lead to an $r^2$ generally 0.60. MSY ( 0.07 to 0.90 moose/10 km$^2$), and optimum effort (3 to 19 hunting-days/10 km$^2$) varies considerably from one reserve to the next (Table 3), indicating regional differences in potential.

Data from the 12 zecs show that surplus-yield models can also be applied to these territories (Table 4). While the models are generally significant ($P \leq 0.05$), $r^2$ are lower for zecs than for reserves. MSY variability is

Table 3.Optimal parameters of moose hunting in Québec wildlife reserves using the model giving the greatest coefficient of determination ($r^2$). n = number of harvest seasons; H-D = number of hunting-days; $r^2$ = coefficient of determination; P = level of signifiance

| Region | Wildlife reserve ($km^2$ of hunted area) | Model | n | $r^2$ | P | Optimal hunting effort (H-D/10 $km^2$) | Observed hunting effort [1] (H-D/10$km^2$) | Optimal harvest (moose/10$km^2$) | Observed harvest [1] (moose/10$km^2$) |
|---|---|---|---|---|---|---|---|---|---|
| South - eastern | Chics-chocs (939 $km^2$) | Fox | 5 | 0.64 | 0.1062 | 15 | 10 | 0.52 | 0.15 |
| | Matane (980 $km^2$) | Schaefer | 26 | 0.69 | 0.0001 | 5 | 6 | 0.90 | 0.83 |
| Central | Mastigouche (1,574 $km^2$) | Schaefer | 17 | 0.70 | 0.0001 | 19 | 14 | 0.44 | 0.46 |
| | Portneuf (774 $km^2$) | Schaefer | 21 | 0.88 | 0.0001 | 13 | 15 | 0.41 | 0.36 |
| | Rouge-Matawin (1,307 $km^2$) | Fox | 18 | 0.88 | 0.0001 | 5 | 10 | 0.45 | 0.35 |
| | Saint-Maurice (786 $km^2$) | Schaefer | 21 | 0.60 | 0.0001 | 7 | 13 | 0.42 | 0.32 |
| Western | La Vérendrye (10,274 $km^2$) | Fox | 19 | 0.93 | 0.0001 | 3 | 5 | 0.19 | 0.16 |
| North - central | Laurentides (5,137 $km^2$) | Fox | 28 | 0.89 | 0.0001 | 4 | 7 | 0.28 | 0.27 |
| | Ashuapmushuan (1,003 $km^2$) | Schaefer | 14 | 0.22 | 0.0943 | 8 | 10 | 0.19 | 0.15 |
| Northern | Sept-Iles/Port Cartier (1,197 $km^2$) | Fox | 6 | 0.31 | 0.2467 | 4 | 4 | 0.07 | 0.09 |
| Total | All the reserves combined (23,971 $km^2$) | Fox | 28 | 0.93 | 0.0001 | 4 | 7 | 0.25 | 0.26 |

[1]Mean for 1987 - 1989

somewhat less pronounced between zecs (0.23-0.92 moose/10 km$^2$; Table 4) than between reserves but optimum effort (16-85 hunting-days/10 km) is more variable. MSY is also higher in zecs ($\bar{x}$ = 0.44 moose/10 km$^2$) than in reserves ($\bar{x}$ = 0.25 moose/10 km$^2$), but hunting effort by unit area necessary to achieve MSY is about eight times greater in zecs (31 hunting-days/10 km$^2$) than in reserves (4 hunting-days/10 km$^2$). Differences in MSY between zecs and reserves can be explained by the fact that the zecs studied are all located in central Québec whereas the 10 reserves are equally distributed throughout the province.

## DISCUSSION

Exponential hunting effort growth in wildlife reserves over the last 30 years is indicative of the situation in all Québec hunting zones. However, the harvest reached its maximum more rapidly outside reserves as shown in zecs. There, less restrictive hunting regulations permitted higher harvest rates which have led to important density declines in several territories (Courtois and Lamontagne 1990; Courtois 1991).

Hunting statistics (harvest, % males, % yearlings , etc.) were successfully used to evaluate moose status outside reserves (Courtois and Lamontagne 1990). In these areas, the impact of hunting was sufficiently high to imprint tendencies in biological indices which are then correlated to population parameters (Crête and Dussault 1986; Courtois *et al.* 1991; Courtois and Crête 1993). In wildlife reserves, except for the yearling %, no significant trends in the biological indices were ascertained in spite of a substantial increase in the harvest. Bouchard and Moisan (1974) also noted an increase in the yearling % in Laurentides reserve after about 10 years of harvesting, a change they believed attributable to a productivity increase. They also reported a lowering of the mean age but this trend did not persist.

Contrary to biological indices, harvest characteristics changed consistently over the last 30 years as shown by high correlations between those parameters and time. The harvest per unit of effort changed markedly with increase of hunting effort permitting the application of surplus-yield models. Identification of the MSY and the optimal hunting effort values were, as a result, possible, a prediction that biological indices did not permit. This is particularly useful because moose harvest rarely declines rapidly immediately after the harvest exceeds MSY, hunters tending to increase their hunting effort (e.g. effective hunting time) or hunting techniques (e.g. ATV, communication system, number of observing sites, etc.) to improve their hunting capacity. This tends to maintain high harvest while the population declines below its optimal density.

Surplus-yield models were initially developed for populations limited by food and for which a density decline should be followed by a productivity (birth rate, pregnancy rate, fetuses / female, etc.) increase. This particular situation could act in regions where the wolf (*Canis lupus*) is absent (southern Québec; Crête 1987) or where its impact is marginal as suggested by high calf / female in harvest (Courtois and Crête 1993) or in aerial surveys (Courtois 1991). In western Québec, predation is an important component of the moose population dynamic which could theoretically limit the application of surplus-yield models. However, we computed significant models for La Vérendrye reserve located in that part of Québec. Messier (1985) and Messier and Crête (1985) showed that predation tends to diminish due to an increased searching time when moose density declines thus improving recruitment (calf survival). We believe that such a mechanism could help to produce a harvestable surplus after introducing harvest in predator-limited populations.

Schaefer's and Fox's models seem in general reliable as shown by $r^2 \geq 0.60$ in 8 of the 10 reserves studied. Determination coeffi-

Table 4. Optimal parameters of moose hunting in Québec zecs using the model giving the greatest coefficient of determination ($r^2$). n = number of harvest seasons; H-D = number of hunting-days; $r^2$ = coefficient of determination; P = level of signifiance

| Region | Zecs ($km^2$ of hunted area) | Model | n | $r^2$ | P | Optimal hunting effort (H-D/10 $km^2$) | Observed hunting effort [1] (H-D/10$km^2$) | Optimal harvest (moose/10$km^2$) | Observed harvest [1] (moose/10$km^2$) |
|---|---|---|---|---|---|---|---|---|---|
| Central | Bessonne (497 $km^2$) | Schaefer | 11 | 0.49 | 0.0158 | 68 | 60 | 0.66 | 0.56 |
| | Borgia (567 $km^2$) | Fox | 11 | 0.74 | 0.0007 | 45 | 47 | 0.49 | 0.43 |
| | Chapeau-de-Paille (807 $km^2$) | Fox | 10 | 0.54 | 0.0149 | 70 | 78 | 0.71 | 0.69 |
| | La Croche (234 $km^2$) | Fox | 11 | 0.36 | 0.0508 | 65 | 37 | 0.73 | 0.43 |
| | Flamand (301 $km^2$) | Schaefer | 10 | 0.37 | 0.0616 | 33 | 30 | 0.50 | 0.70 |
| | Frémont (572 $km^2$) | Schaefer | 12 | 0.55 | 0.0058 | 16 | 16 | 0.23 | 0.25 |
| | Gros-Brochet (752 $km^2$) | Schaefer | 12 | 0.44 | 0.0179 | 28 | 30 | 0.41 | 0.42 |
| | Jeannotte (361 $km^2$) | Fox | 11 | 0.64 | 0.0030 | 63 | 45 | 0.91 | 0.63 |
| | Kiskissink (686 $km^2$) | Fox | 10 | 0.66 | 0.0043 | 37 | 32 | 0.92 | 0.50 |
| | Ménokéosawin (314 $km^2$) | Fox | 11 | 0.45 | 0.0231 | 61 | 42 | 0.61 | 0.55 |
| | Tawachiche (227 $km^2$) | Schaefer | 11 | 0.49 | 0.0167 | 85 | 101 | 0.70 | 0.65 |
| | Wessonneau (912 $km^2$) | Fox | 11 | 0.57 | 0.0069 | 36 | 26 | 0.37 | 0.33 |
| | All the zecs of the central region combined (6,230 $km^2$) | Fox | 11 | 0.68 | 0.0018 | 31 | 36 | 0.44 | 0.42 |

[1] Mean for 1987 - 1989

cients ($r^2$) for surplus-yield models were however weak for some territories, particularly for Ashuapmushuan reserve and some zecs, a situation probably related to imprecision or inconsistency during data collection. This can be partly corrected by the substitution of raw harvest and effort data by a 3-point moving average. For example, determination coefficient for Ashuapmushuan reserve increased from 0.22 ($P = 0.0943$) to 0.59 ($P = 0.0037$) using this technique. Some precision can also be gained with this method for zecs La Croche ($r^2 = 0.43$, $P = 0.0569$) and Flamand ($r^2 = 0.58$, $P = 0.0475$). However, such an approach can preclude data independency. Moose cohorts are exploited during several years so harvest from one year may be influenced by previous years hunting effort. This may be another source of imprecision. Gulland (1971) and Fox (1974 *in* Laloë 1990) suggest replacing hunting efforts by their moving averages, the number of points included in the averages depending on the number of years the cohorts are exploited. Nevertheless, strong correlations between the 5 hunting effort indices studied suggest that it is worthwhile to use the simplest and the most intuitive indices. This facilitates data collection and, in this way, can help to give more accurate results particularly when data are collected by non-specialized personnel as is often the case in zecs.

Surplus-yield results can be used to evaluate the situation of moose populations and to suggest adjustments in some reserves and zecs. Between 1987 and 1989, Québec wildlife reserves observed moose harvests of 0.26 moose/10 km$^2$ and a mean of 7 hunting-days/ 10 km$^2$ suggesting that the potential MSY projected by the surplus-yield models has been reached. Modifications necessary to optimize effort and harvest in each territory can be deduced by comparing recent data to the optimum parameters. This shows that hunting effort is too high in La Vérendrye, Rouge-Matawin and Saint-Maurice reserves. Those territories appear overharvested since their harvest is less than the predicted MSY, and effort is greater than that predicted by the model. On the other hand, effort and harvest could be increased in Chic-Chocs reserve and Jeanotte, Kiskissink and Ménokéosawin zecs.

Surplus-yield models could also help to define regional differences in MSY and in such a way to set targets helpful to moose managers. Using cluster analysis applied to harvest characteristics and biological indices, Courtois and Crête (1993) defined five relatively homogenous groups of management units in Québec that we called regions for the purpose of this paper. Based on results obtained in the reserves, it becomes possible to define the order of magnitude for MSY in these 5 groups of hunting zones. Results from reserves Chic-Chocs and Matane suggest that MSY is between 0.52 and 0.90 moose/10 km$^2$ in the south-eastern part of Québec. Based on Mastigouche, Portneuf, Rouge-Matawin and Saint-Maurice data, MSY could be situated at about 0.41-0.45 moose/10 km$^2$ in the central part of the province. Maximum sustainable yield seems lower in the western (0.19 moose/ 10 km$^2$) and north-central (0.19-0.28 moose/ 10 km$^2$) parts of the province as suggested by the La Vérendrye results and those from Laurentides/Ashuapmushuan respectively. The estimate made in the Sept-Iles/Port-Cartier reserve shows that MSY is at its lowest in the northern portion of the province. Regional differences can be explained by a gradual decline in deciduous twig productivity from south to north (Crête 1989; Courtois and Crête 1993) and a more pronounced impact of predators in western Québec (Crête 1987). Estimated values are probably somewhat underestimated because moose populations in reserves help to sustain hunting in territories adjacent to them via emigration of young animals and adults whose home range is partly outside reserve borders (Goudreault 1980; Jolicoeur and Crête 1988; Desrosiers *et al.* 1989).

MSY estimates calculated from surplus-yield models conform to those computed using other techniques. Fox's model suggests an optimal harvest of 0.19 moose/10 km$^2$ for La Vérendrye reserve which compares with estimates suggested by the models developed by Crête *et al.* (1981) (0.19-0.28 moose/10 km$^2$) for moose populations from the same area. Goudreault and Milette (1984) applied different hunting pressure to moose population in 6 experimental sites of central Québec and they found a MSY of about 0.45 moose/10 km$^2$. This estimate is also similar to the 0.41-0.45 moose/10 km$^2$ calculated from our surplus-yield models for the same area.

Schaefer's model better suited the harvest data of Mastigouche, Saint-Maurice and Portneuf reserves, situated in the central part of Québec, and this model suggests a MSY of about 0.43 moose/10 km$^2$ and an optimal effort of less than 19 hunting-days/10 km$^2$. In most of the studied zecs, located in the same region, greater $r^2$ are given by Fox's model. Estimated MSY is similar (0.44 moose/10 km$^2$) but optimal hunting effort (31 hunting-days/10 km$^2$) is three times that suggested for reserves of central Québec ($\bar{x}$= 11 hunting-days/10 km$^2$). As a result, Schaefer's model, which predicts a sharp decline in harvest when hunting effort is high, seems to correctly fit harvest data mostly when effort is low as is the case in reserves as on such occasions the relation between harvest by unit of effort and effort is still in the linear part of the equilibrium curve. Data from the zecs suggest that this model can be too restrictive. Fox's model indicates that very high hunting efforts are needed to provoke a harvest decline.

## MANAGEMENT IMPLICATIONS

Two strategies seem well adapted to the Québec context. Moose management could be oriented through maximum sustainable yield in reserves where moose densities are near optimal ($\approx$ 0.6 K; Crête *et al.* 1981) and where hunters look for quality in terms of hunting success, exclusive territories as well as accommodations. In other territories, moose densities are generally very far from those giving MSY, particularly in the southern part of Québec where populations are not limited by predation. Regulations necessary to allow moose populations to grow rapidly towards optimum density would be strongly restrictive for hunters. This could displease them and lead to economic loss. Outside reserves and over the short term, it should be pertinent to take into consideration socioeconomic objectives such as fulfilling a high recreation demand or self-financing in zecs at the same level as biological objectives (optimum yield concept; Anderson 1975, Caughley 1976, Larkin 1977). Over the long term, the MSY concept could be relevant in all territories, particularly if the number of hunters declines in the future. In such a situation, we argue that a high quality hunt could be necessary to maintain hunter's interest.

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