# IMPACT OF WOLF AND BLACK BEAR REMOVAL ON COW:CALF RATIO AND MOOSE DENSITY IN SOUTHWESTERN QUÉBEC

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Abstract: Over 4 winters, 7 to 13 wolves were removed annually from a study area and a surrounding buffer zone covering together 2150 $km^2$ in La Vérendrye Game Reserve. In an adjacent 360-$km^2$ block, 25 to 30 black bears were removed every June over 3 consecutive years. Fall estimates indicated that wolf density was reduced to approximately 1 animal 100 $km^{-2}$ in the removal area, as compared to 1.5 wolves 100 $km^{-2}$ in the control block. Bear density was not estimated but females were severely affected by the removal. Trapping effort (days-trap/capture) for female bears increased from 35 to 109 from the first to the third year, while the mean age dropped from 8.5 to 3.3 years. Male harvest was more stable. Observation of radio-tagged female moose probably underestimated birth rate and calf mortality. Based on January cow:calf ratios, moose calf survival in the wolf removal block exceeded the one in the control area in 2 years out of 4, but the difference was statistically significant only in 1 case. Calf survival was significantly higher in the bear removal area than in the control block in 2 winters out of 3. It was impossible to detect a clear response to the treatment for moose density. The inconclusive results can be explained by too weak a treatment, annual and regional variations, sampling errors, limited sample sizes, small and close study areas.





Résumé: Au cours de 4 hivers, de 7 à 13 loups furent éliminés annuellement d'un secteur expérimental et d'une zone tampon périphérique qui couvraient ensemble 2150 $km^2$ de la réserve faunique de La Vérendrye. Dans un secteur adjacent de 360 $km^2$, entre 25 et 30 ours furent capturés en juin au cours de 3 années consécutives. Des estimations automnales indiquèrent que la densité de loup fut diminuée à approximativement 1 individu 100 $km^{-2}$ dans le secteur expérimental, comparativement à 1.5 loups 100 $km^{-2}$ dans le secteur témoin. La densité de l'ours ne put être estimée mais les femelles furent sévèrement affectées par le programme. Dans leur cas, l'effort de piégeage (jours-piège par prise) augmente de 35 la première année à 109 la troisième, alors que leur âge moyen chuta de 8.5 à 3.3 ans. La capture de mâles fut plus stable. L'observation d'orignales munies de collier-émetteur produisit des estimations probablement biaisées du taux de naissance et de survie des faons. D'après le nombre de faons observés par femelle en janvier, la survie des faons dans le secteur de capture des loups dépassa celle du secteur témoin 2 ans sur 4, mais la différence n'était statistiquement significative qu'une seule fois. La survie des faons était significativement supérieure dans le secteur de retrait des ours que dans le secteur témoin au cours de 2 années sur 3. Il fut impossible de détecter une réponse claire au traitement de la densité d'orignaux. Ces résultats non concluants furent attribués à un traitement trop faible, à des variations annuelles et régionales, à l'erreur échantillonnale, à des tailles-échantillons limitées à la petitesse et la proximité des aires d'étude.

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Among North-American jurisdictions, hunting pressure exerted on moose (*Alces alces*) has reached its highest value in Québec in recent years (Crête 1987). Over 140 000 hunting licences have been sold annually, even though the total pre-hunt moose population is estimated at 70 000 animals, yielding a harvest of 11 000 head. The demand is high and moose management has been oriented towards maintaining a difficult balance between an increasing pressure and a limited harvest.

With the advent of telemetry, predation by wolf (Canis lupus), black bear (Ursus americanus) and grizzly bear (U. arctos) was recognized as a major cause of death among moose in different areas, particularly during the few months following birth (Franzmann et al. 1980; Ballard et al. 1981; Hauge and Keith 1981; Gasaway et al. 1983; Crête and Messier 1984). Experimental removal of wolves (Gasaway et al. 1983; Crête and Messier 1984) and black bears (Stewart et al. 1985) produced an immediate increase in calf survival.

Available data suggest that predation by wolf can be density dependent (Messier and Crête 1985), and when combined with bear predation, could regulate moose numbers by trapping populations in a "predator pit" (Haber 1977; Messier and Crête 1985). Crête (1987) hypothesized that the presence of two predators (wolf and one species of bear) was necessary for a predator pit to exist. Growth curves producing predator pits indicate that increased harvestable surplus could be possible if predation was temporally reduced.

Moose density appears to level off at 4-5 animals 10 $km^{-2}$ in southwestern Québec in the absence of hunting by humans (Crête et al. 1981; Messier and Crête 1985; Crête 1987). However, the annual



production of deciduous browse, a major element in the determination of K carrying capacity (KCC; Macnab 1985) for moose habitat, would suffice to sustain 36 to 60 moose 10 $km^{-2}$ (Crête 1988). A predator pit could then exist at a density one order of magnitude lower than KCC.

While hunting pressure has been heavy on moose, the capture of wolves by trappers has not been attractive in Québec because of the low value of the pelts in relation to the difficulty of capturing this species. In addition, trappers have not paid much attention to black bear in recent decades. Moreover, the black bear has not yet reached a widespread status as big game and trophy animal among Québec hunters, so the species recieves three times less hunting pressure than moose. This unbalanced exploitation of moose and its predators could have modified a possible pristine equilibrium.

We tested the hypothesis that predation by wolves and black bears has kept moose populations below KCC in La Vérendrye Game Reserve, despite little hunting by humans. Higher calf survival and increasing density following predator reduction would support the hypothesis. If it were true, we would try to simultaneously manage, through hunting and trapping regulations, moose, black bears and wolves so that moose numbers and harvests by humans could increase.

## STUDY AREA

Three areas of La Vērendrye Game Reserve were used to test the hypothesis: a 700-km$^2$ block where wolves were removed (WRB), a 360-km$^2$ area for experimenting black bear removal (BRB) and a control block (CB) covering 900 km$^2$ (Fig. 1). The study area is hilly, typical of the Canadian Shield, with the altitude ranging between 200 and 600 m; lakes and streams are numerous. Habitat is dominated by mixed forests in well drained areas, since La Vērendrye Game Reserve is located in a transition zone between deciduous forests of the St.-Lawrence Valley and the northern conifer forests. Dominant tree species are white and yellow birch (Betula papyrifera and B. alleghaniensis), sugar maple (Acer saccharum), trembling aspen (Populus tremuloides), balsam fir (Abies balsamea), white and black spruce (Picea glauca, P. mariana) and white pine (Pinus strobus). Habitat is more boreal in WRB than in the 2 other blocks; it lacks extensive maple-yellow birch stands. Logging of spruces, white pine, yellow birch, and to a lesser extent balsam fir and sugar maple has been common for many decades in the reserve. Crête (1977) described the impact of logging on moose habitat in the region. Annual deciduous and balsam fir browse production were estimated respectively at 31 and 5 kg ha$^{-1}$ (dry weight) in WRB (Crête and Jordan 1982). Comparable figures do not exist for BRB and CB, but field impressions suggest they differ little.

Since the beginning of the sixties, moose density appears to have remained relatively stable at 3-4 animals 10 km$^{-2}$ in the reserve (Messier and Crête 1984). There has been a controlled hunt (Bouchard



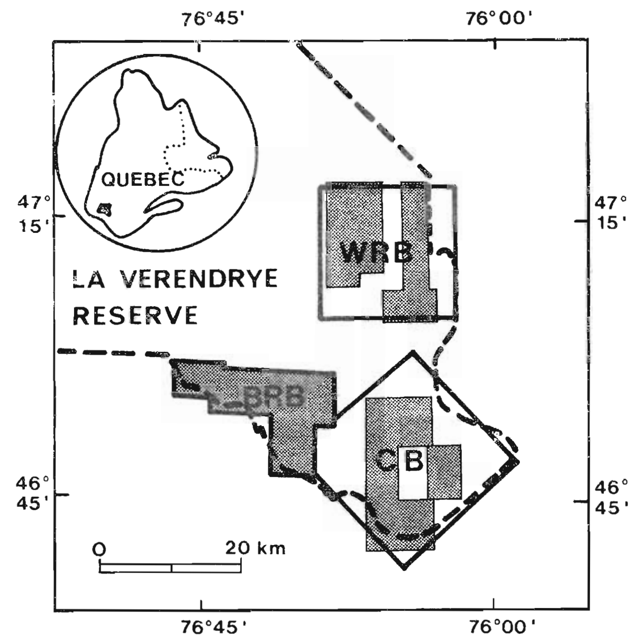


Figure 1. Location of La Vērendrye Game Reserve in southwestern Québec where the impact of wolf (WRB) and black bear (BRB) removal on moose was studied; CB = control block. Shaded areas indicate position of plots covered during aerial surveys.

and Moisan 1974) since 1964 with limited entry; hunting pressure has been kept low as compared to adjacent general areas (Crête et al. 1981; Crête and Jolicoeur 1985), and annual harvest rate was estimated at 4 percent (Messier and Crête 1984). There has been some subsistance hunting done by Algonquins that inhabit La Vérendrye Game Reserve outside of the study area; their harvest is not reported but seems limited and restricted to major roads.

Besides moose, white-tailed deer (Odocoileus virginianus) are relatively common in CB, mainly during the snow-free period; they are less abundant further north in the 2 other blocks. Major wintering areas occur 10-50 km southeast of La Vérendrye Game Reserve and wolf packs inhabiting CB may visit them (Messier 1985a). However white-tailed deer do not exceed 6 percent of wolf diet in any season in CB (Messier and Crête 1985).

Wolf ecology was studied in CB between 1980 and 1984 (Messier 1985a, b), and density ranged between 1.2 and 1.5 individuals 100 $km^{-2}$ during this period. Moose composed more than half of the wolf diet in all seasons. Wolves have also been common elsewhere in La Vérendrye Game Reserve for years at probably similar densities. Wolves have been lightly harvested by trapping in the study area and collision with vehicles has been almost as important a mortality factor as trapping (Messier 1985b). Black bears are also common and lightly harvested in the reserve: a minimum density of 2.3 animals 10 $km^{-2}$ was estimated for part of CB in 1982 (Lachapelle et al. 1984). Scat analysis of black bear indicated rare occurence (1 percent) of moose hair or hoof



(Lachapelle et al. 1984); however this technique may fail to fully evaluate the importance of bear predation on moose (Wilton et al. 1984).

## METHODS

Wolves were captured either by trapping or by shooting from a helicopter for 4 years between October 1981 and March 1985. Considering the large size of pack territories (390 $km^2$; Messier 1985b) in relation to WRB, wolves were also reduced from a 10-km wide buffer zone surrounding WRB: total removal area covered 2150 $km^2$. Trapping was performed during the regular trapping season in fall, east of the Game Reserve in the buffer zone, by persons associated with project personnel. It is unlikely that wolf trapping occurred in the area before the outset of the experiment. Wolves were also shot from a helicopter after tracking them in the snow, between December and March of each year. Some animals whose tracks were detected in WRB or the buffer zone, were finally captured outside the buffer zone.

Black bears were trapped from late May to mid-June in 1983, 1984 and 1985. Two types of footsnare traps and New House # 114 steel traps were used the first year; only footsnares were utilized thereafter. Trapping effort was adjusted to take into account differential efficiency of the 3 models of traps used, and was expressed in terms of the most efficient snare. Sometimes traps did not retain large bears, particularly during the first year, and adjustments to snares had to be made. Traps were checked daily and captured animals were killed with a rifle.

Bears were weighted and their age determined by histological count of cementum annuli.

For each block, wolf density was estimated by averaging predictions made with 3 validated indices derived from moose hunter interviews (Crête and Messier 1987): percentage of hunters observing wolf tracks, percentage of hunters observing wolf scats, and percent of days howling was reported. No validated indices of black bear abundance were available; we used the trapping effort (days-trap per capture) to estimate the trend of bear density in BRB.

Survival of moose calves was estimated in 2 ways in each block: from telemetry and from winter aerial surveys. Seven to 13 radio-collared adult females per block, were located from a helicopter. They were monitored daily for about 10 days during parturition (May 20-30) and at 1-2 month intervals thereafter. The animals were observed in all cases when leaves were absent, but only about 50 percent of the time in summer. The number of associated calves was noted when the cow was observed; if a calf ceased to be observed with a female on at least 2 consecutive occasions, it was presumed dead. Moose calves are seen 90 percent of the time when their dam is observed (Hauge and Keith 1981). Observations from different years were pooled because of small sample sizes.

Calf survival was also compared between blocks by determining cow:calf ratios during January of each year. Surveys were conducted from a helicopter. Observed moose occupied randomly selected plots used



for density estimates. Their sex and age (calf or adult) were determined by the presence of antlers or vulval patch and relative size (Crête and Goudreault 1980). Surveys were flown from 1981 to 1986 in WRB and CB and from 1984 to 1986 in BRB. Sample sizes were progressively increased with years in order to produce more accurate estimates. Standard errors of ratios were calculated according to Czaplewski et al. (1983).

Moose density was estimated in January of each year from aerial counts done in helicopter (Crête and St-Hilaire 1979). Moose tracks were first located with a fixed-wing aircraft and subsequent helicopter searches were restricted to track networks. A visibility rate of 70 percent was used to correct density estimate (Crête et al. 1986; unpubl. data). Estimates were derived from sampling with 60-$km^2$ plots (Crête and St-Hilaire 1979); until 1984, 4 permanent plots were randomly allocated per block, while 6 were used thereafter. On a few occasions, some plots could not partly or totally be covered by the helicopter; density was then extrapolated with the ratio moose/$km^2$ of track networks found in the rest of the block for a given year.

## RESULTS

### Predator Removal

The number of wolves removed in WRB varied between 7 and 13 during the winters 1981-82 through 1984-85 (Table 1; Fig. 2); this represents

Table 1. Number of wolves and black bears removed from the study area in La Vêrendrye Game Reserve between 1981 and 1985. Wolves were captured between October and March, and bears were trapped in June.

| area | 1981-1982 | 1982-1983 | 1983-1984 | 1984-1985 |
|---|---|---|---|---|
| Wolf removal | | | | |
| from helicopter | 8(6[a]) | 4(4) | 8(6) | 7(5) |
| by trappers | 5(0) | 5(0) | 3(1) | 0 |
| Black bear removed | No removal | 30 | 26 | 25 |

[a] number of wolves ≥ 1 year old

a harvest of 0.3-0.6 animals 100 $km^{-2}$. The majority of the removal was done using helicopter. Adults ( ≥ 1 years old) dominated among wolves shot from the air, while trapping was highly biased towards young. The sex-ratio was close to parity in both samples, with a combined total of 20 males and 19 females (the sex of one trapped animal was unknown). According to our field observations, no permanent large pack used WRB after the first year.

Wolf removal apparently affected their numbers as the estimated density dropped from 2.1 individuals 100 $km^{-2}$ in the fall before the outset of the experiment to 0.8-1.1 afterwards (Table 3). During the same period, estimated density remained relatively stable at about 1.5 wolves 100 $km^{-2}$ in CB. Annual low in wolf numbers reached a minimum during late winter upon completion of removal efforts. Colonizing animals probably came back progressively to WRB. Since the density was





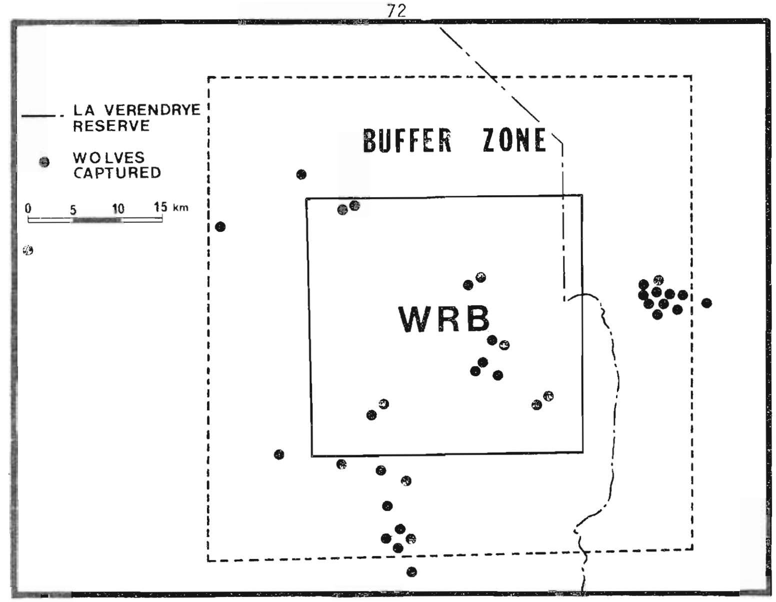


Figure 2. Location of wolves captured between October 1981 and March 1985 in the study area.

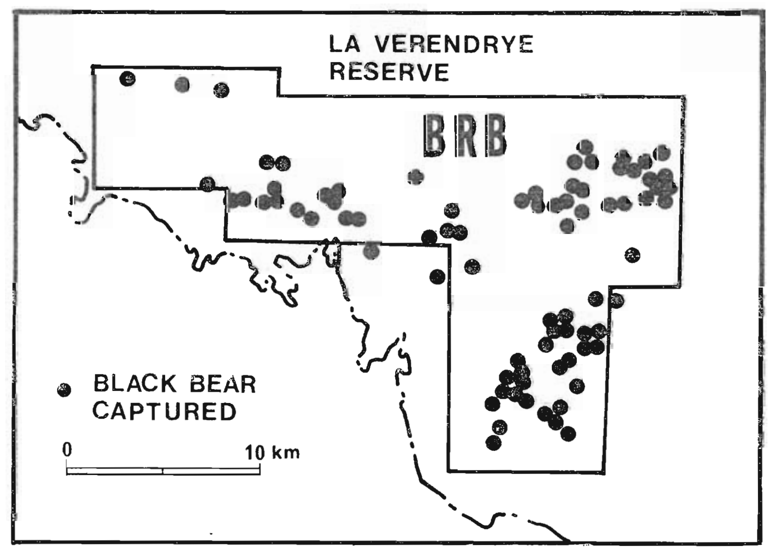


Figure 3. Location of black bears trapped in the study area between 1983 and 1985.

Table 2. Mean (SE) age (years) and weight (kg) of captured bears, according to their sex and year, La Vérendrye Game Reserve, Québec. Cubs were excluded from computation because we were unable to find them the first year.

| | males | | | females | | |
|---|---|---|---|---|---|---|
| | 1983 | 1984 | 1985 | 1983 | 1984 | 1985 |
| Mean age | 3.1(0.7) | 3.6(0.5) | 3.8(1.2) | 8.5(1.5) | 4.8(1.0) | 3.3(0.3) |
| Mean weight | 54.5(11.0) | 59.3(10.5) | 52.4(7.5) | 46.7(3.2) | 37.3(3.8) | 39.8(4.1) |
| Yearlings captured | 11 | 10 | 15 | 19 | 16 | 8 |
| Cubs captured | 0 | 0 | 1 | 0 | 0 | 1 |



estimated in fall before trapping season, the reduction in predation pressure on moose calves during summer could have exceeded the apparent estimate of one third suggested by Table 3. Wolf density in BRB could also have diminished (Table 3); considering the proximity of BRB and the buffer zone of WRB, some wolves inhabiting the former block were probably captured in the latter. This happened for a wolf that was previously marked in BRB; however, we do not know if it was a case of dispersion or extraterritorial movement (Messier 1985a).

The number of black bears taken in BRB decreased from 30 in 1983 to 25 the third year (Table 1; Fig. 3), a harvest of 0.7-0.8 animal 10 $km^{-2}$. The downward trend was caused by the decline of females (Table 2). Adult females represented a smaller proportion of the harvest after the first year. Their mean age dropped significantly ($\underline{t}$=2.05; $\underline{P} < 0.05$) between the first and second year; a similar trend was detectable for carcass weight ($\underline{t}$=1.88; $\underline{P} < 0.1$). The age and the weight of males exhibited a larger variance and revealed no trend during the 3 summers; the difficulty of capturing large animals the first year may explain the results.

Bear trapping intensity reached 673 days-trap the first year, 948 the second, and 875 in 1985. For females, the trapping effort almost doubled every year, from 35 days-trap per capture in 1983, to 109 in 1985. On the other hand, trapping effort was more variable for males. These results suggest that resident female black bears in BRB were severely reduced by our trapping, while the males, that wander on larger home range (Young and Ruff 1982), were less affected. Moreover the

Table 3. Mean number of wolves 100 $km^{-2}$ as predicted from the average of three indices of wolf density (percentage of moose hunters having observed wolf scats or tracks, and number of days wolf howls heard: Crête and Messier 1987), according to three areas of La Vérendrye Game Reserve where removal of moose predators was studied between 1981 and 1986. Wolf removal began in October 1981 and black bear removal in June 1983.

| | 1981 | 1982 | 1983 | 1984 | 1985 |
|---|---|---|---|---|---|
| Control area | 1.4 | 1.6 | 0.8 | 1.5 | 1.4 |
| Wolf removal area | 2.1[a] | 0.9 | 1.1 | 0.8 | 1.0 |
| Bear removal area | NA[b] | NA | 1.5 | 1.2 | 1.1 |

[a] pretreatment
[b] not available

difficulty of trapping large animals during the first season could have delayed the removal of males.

Calf Survival and Moose Density

Approximately 80 newborn calves per 100 cows were observed with radio-equipped females in CB and WRB during the study period; this ratio exceeded 110 in BRB, but the difference was not statistically significant (Table 4: chi-square=0.76; $P > 0.5$). According to the calves observed with monitored females, overall survival rates were not statistically different in the 3 blocks, from May to November (chi-square=1.15; $P > 0.5$), and from November to March (chi-square=1.82; $P > 0.25$). Most calves disappeared during summer, as was previously





Table 4. Number of calves produced by radio-collared female moose (mostly adults) and survival of these young during their first ten months of life, as determined by radio tracking in helicopter, according to three areas of La Vérendrye Reserve where removal of moose predators was studied between 1981 and 1986.

| | Calves born/ 100 females | Survival rate of calves | |
|---|---|---|---|
| | | May-November | November-March |
| Control area | 73(32[a]) | 0.65(20[b]) | 0.88(8[b]) |
| Wolf removal area | 84(32) | 0.58(24) | 1.00(11) |
| Black bear removal area | 113(15) | 0.46(13) | 1.00(3) |

[a] Number of births observed
[b] Number of calves monitored

documented in the study area (Crête and Messier 1984), and close to 50 percent survived to the age of 10 months. However, estimated survival rates could be biased upwards if some cases of death were missed immediately after birth. This possibility cannot be ruled out, particularly for CB and WRB, because observed birth rates were lower than predictions derived from ovulation rates. Ninety-three out of 96 instances of telemetry observation during parturition concerned females $\geq$ 3 years old; their ovulation rate should reach 130-140 per 100 cows in Québec according to ovary examination (Crête and Beaumont 1986).

The impact of wolf removal, that began during the winter 1981-1982, should have produced a higher cow:calf ratio starting with the 1983 aerial survey; on the other hand, reduction of bear numbers should have begun to affect cow:calf ratios in the winter 1984. During the 2 years which preceeded wolf removal, cow:calf ratios varied greatly in CB and WRB, but the differences were not significant ($t$ test; $P > 0.1$: Table 5). For the 4 years of wolf removal, the cow:calf ratio in WRB exceeded the one in CB in 2 winters, but only in 1985 was the difference statistically significant (one-tailed $t$=2.14; $P < 0.025$). The cow:calf ratios in BRB almost doubled the ones in CB in 2 aerial surveys out of 3; however the tendency for an increase was weak in 1984 (one tailed $t$= 1.60; $P < 0.1$), but more significant in 1986 ($t$=3.6; $P < 0.001$).

Even with a sampling fraction approaching 50 percent in WRB and CB (100 percent in BRB), precision of density estimates was low (Table 6). In both areas, there was an apparent trend for increasing density during the first part of the study, with a reduction afterward. The trend appeared more pronounced in WRB. Two strong cohorts born in 1980 and 1982 (aerial survey of 1981 and 1983: Table 5) could have allowed the density to increase between 1981 and 1984 in CB. In WRB, 2 good years and one moderate one for calf survival produced an increase in density between 1982 and 1985. In 1978, corrected density was estimated at 3.9 moose 10 $km^{-2}$ in WRB (Crête et al. 1981). Finally, BRB data are too limited and too imprecise for the first year to detect changes in density.

## DISCUSSION

Predator numbers were clearly affected by the removal in WRB and BRB. Wolf density was kept at least one third lower than in CB, and no



Table 5. Mean (SE; $n$) number of moose calves per 100 females observed from helicopter in January according to three areas of La Vérendrye Game Reserve where removal of moose predators was studied between 1981 and 1986. Wolf removal began in October 1981 and black bear removal in June 1983.

| | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 |
|---|---|---|---|---|---|---|
| Control area | 65(18[a];43[a]) | 24(7;56) | 45(11;56) | 30(7;74) | 18(5;67) | 25(5;99) |
| Wolf removal area | 30(11;35) | 52(15;38) | 68(18;47) | 32(9;50) | 40(9;81) | 19(4;105) |
| Bear removal area | NA[b] | NA | NA | 58(16;30) | 22(4;50) | 62(9;55) |

[a] computed according to Czaplewski et al. (1983)

[b] not available

Table 6. Corrected mean (SE; $n$) moose density (animals 10 $km^{-2}$) estimated from helicopter counts in January according to three areas fo La Vérendrye Game Reserve where removal of moose predators was studied between 1981 and 1986.

| | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 |
|---|---|---|---|---|---|---|
| Control area | 4.1(0.9;4) | 4.4(0.9;4) | 4.9(0.8;4) | 5.6(1.4;4) | 5.4(0.6;6) | 4.0(0.6;6) |
| Wolf removal area | 3.6(1.1;4) | 3.7(0.8;4) | 4.1(0.5;4) | 4.3(0.6;4) | 6.2(0.9;6) | 5.0(0.8;6) |
| Bear removal area | NA | NA | NA | 2.6(0.4;4) | 3.2(0.1;6) | 3.0(0.1;6) |

large packs could establish a territory in the area after the winter of 1982. Black bear density, particularly female numbers, decreased in BRB, as trapping effort increased over the 3 years. However the results do not allow us to reject the null hypothesis. Even with a massive annual investment of 250-300 days-person and 100-150 helicopter hours, it was impossible to show clearly that high calf mortality was attributable to black bear and wolf predation. Too weak a treatment, annual and regional variations, sampling error, limited sample size, small and close study areas are all reasons that explain why it was difficult to detect a treatment effect.

Two removal experiments, one with wolves in Alaska (Gasaway et al. 1983), and one with black bears in Saskatchewan (Stewart et al. 1985), illustrate that our removal was not pronounced enough to produce a sharp increase in calf survival and density. In Alaska, there were 12 to 16 moose per wolf before the experiment and wolf predation severely affected recruitment. Moreover 20 percent of adults were killed annually by wolves during this period. At the end of the removal study, the ratio rose to 44 moose per wolf, while predation rate on adults fell to $\leq$6 percent. In CB, every wolf had access to approximately 30 moose during the study, which is above the critical level of 20 proposed by Gasaway et al. (1983); this ratio increased to 45 in WRB. On the other hand, the annual predation rate on adults was estimated at 10 percent in CB, based on wolf density and food habits (Messier and Crête 1985); however observed predation on our monitored females averaged 3 percent (n=65 years-female) in the 3 blocks. Even if one might be cautious with the use of moose:wolf ratios (Messier and Crête 1985), it is probable



that predation pressure exerted by wolves was much lower in La Vérendrye Game Reserve than in the Alaskan study area in addition to the fact that a lower fraction of the wolf population was removed in our study: this explains the weak response observed in WRB.

In the study on black bears carried out in Saskatchewan (Stewart et al. 1985), 1.3 and 1.8 bears 10 $km^{-2}$ were removed during 2 consecutive years at 2 different locations. Adult males dominated among killed bears. Bear density was unknown, but 19 and 24 bears per 100 moose were respectively removed the first and the second year. In BRB, 0.7-0.8 bear 10 $km^{-2}$ were removed, which represented 23 to 33 bears per 100 moose. A minimum density of 2.3 bears 10 $km^{-2}$ was estimated in CB (Lachapelle et al. 1984); however actual density may have been closer to 3-4 bears 10 $km^{-2}$, judging by the comparable trapping effort needed in BRB and in another game reserve with known bear density (Jolicoeur, unpubl. data). Approximately 20-30 percent of the bear population was then removed annually in BRB. If predation behaviour of bears was similar in Saskatchewan and in La Vérendrye Game Reserve, bear density should have been comparable in the 2 areas; the cow:calf ratio in control areas averaged 37 calves per 100 cows in Saskatchewan (including yearling females), and 35 over 6 years in CB. The more pronounced response of calf survival observed in Saskatchewan could have been caused by the higher proportion of the bear population removed there.

The proximity of the 3 blocks may have caused some treatment interactions. A telemetry study of wolves inhabiting CB between 1980 and 1984 (Messier 1985 a, b) indicated that removal in WRB did not affect those animals. However, some wolves using BRB may have been captured in WRB, so that a partially combined treatment may have been applied in BRB. Knowledge of bear movements is limited, but 6 radio-tagged females (Lachapelle et al. 1984) used 10-15 km$^2$ in CB over one year (Crête, unpubl. data). Most of the female black bears removed in BRB were then probably resident of the block, while males, which generally wander over a larger home range (Young and Ruff 1982), may have also used outside areas, particularly the adjacent CB. In this respect, it is important to note that CB sampling plots were not adjacent to BRB (Fig. 1); as a result, a buffer zone existed.

For moose, the estimation of birth rate based on daily monitoring of radio-tagged females during parturition may be biased. Ovulation rate per 100 adult females exceeds 120 in Québec game reserves (Crête and Beaumont 1986). However we only counted 78 and 84 calves per 100 cows respectively in CB and WRB, even though the vast majority of the females was over 2 years old. Hauge and Keith (1981) observed a similar number of calves in an area of Alberta where they suspected black bear predation to be important. However, Stewart et al. (1985) observed comparable ratios in the fall rather than during spring in their experimental areas. It is then likely that black bears kill a fair number of moose calves immediately after birth. Observation of neonate cervid hair in black bear stomach collected in May and June in Ontario (Wilton et al. 1984) support this hypothesis.

Messier and Crête (1985) questioned if black bear predation on moose was density dependent, as wolf predation appeared to be in their study





area. The fact that improved calf survival seemed proportional to the number of bears killed 10 km$^{-2}$ rather than to the number of bears removed per moose would indicate that bear predation is not density dependent. This would make sense as bear density is likely regulated by something else than the density of a very occasional prey. The predator pit where moose populations appear to be trapped in southwestern Québec would then be caused by the combined action of 2 predator species, the wolf whose killing rate seems proportional to moose density (Messier and Crête 1985), and the black bear whose predation rate is independent of moose density. In addition, there could be annual variations in the predation rate of the 2 species; bear removal was associated with higher cow:calf ratio in 1984 and 1986, while wolf removal was in 1985 (Table 5). More research is needed on this possible switching. To further complicate the understanding of the system, overall calf production and/or survival seem to fluctuate annually judging by cow:calf ratios in CB.

Moose habitat is rich in La Vérendrye Game Reserve (Crête and Jordan 1982). Annual forage production could sustain over 30 moose 10 km$^{-2}$ (Crête 1988). Female moose are productive and reach high ovulation rates (Crête and Beaumont 1986). However, very often only 20 to 30 calves per 100 cows survive until January. Calf mortality rate probably exceeds 75 percent in extreme years. We were unable to clearly show that black bear and wolf predation was the cause because of too weak treatments. In order to reach a conclusion regarding the initial hypothesis, bears and wolves should be intensively removed in the same experimental block.

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RERERENCES

BALLARD, W.B., T.H. SPRAKER, and K.P. TAYLOR. 1981. Causes of neonatal moose calf mortality in south central Alaska. J. Wildl. Manage. 45: 335-342.

BOUCHARD, R., and G. MOISAN. 1974. Chasse contrôlée à l'orignal dans les parcs et réserves du Québec (1962-1972). Naturaliste Can. 101: 689-704.

CRÊTE, M. 1977. Importance de la coupe forestière sur l'habitat hivernal de l'orignal dans le sud-ouest du Québec. Can. J. For. Res. 7: 241-257.

CRÊTE, M. 1987. The impact of sport hunting on north american moose. Sweed. Wildl. Res. in press.

CRÊTE, M. 1988. Production of forage and its use by a moose population at high density in eastern Québec: estimation of K carrying capacity. J. Wildl. Manage. (Submitted).

CRÊTE, M., and A. BEAUMONT. 1986. Fécondité de l'orgnal au Québec d'après l'examen macroscopique d'ovaires récoltés au début de l'automne. Alces 22: in press.

CRÊTE, M., and F. GOUDREAULT. 1980. Les bois, la tache vulvaire et la couleur du museau pour déterminer le sexe des orignaux en janvier dans le sud-ouest du Québec. Proc. N. Am. Moose Conf. Workshop 16: 275-288.

CRÊTE, M., and H. JOLICOEUR. 1985. Comparing two systems of moose management for harvest. Wildl. Soc. Bull. 13: 464-469.

CRÊTE, M., and P.A. JORDAN. 1982. Production and quality of forage available to moose in southwestern Québec. Can. J. For. Res. 12: 151-159.

CRÊTE, M. and F. MESSIER. 1984. Influence d'une réduction du nombre de loups sur une population d'orignaux dans le sud-ouest du Québec. Alces 20: 107-128.

CRÊTE, M., and F. MESSIER. 1987. Evaluation of indices of gray wolf density in hardwood-conifer forests of southestern Québec. Can. Field-Nat. 101: in press.

CRÊTE, M., 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: 751-762.

CRÊTE, M., R.J. TAYLOR, and P.A. JORDAN. 1981. Optimization of moose harvest in southwestern Québec. J. Wildl. Manage. 45: 598-611.

CRÊTE, M. and D. ST-HILAIRE. 1979. L'hélicoptère et l'avion pour dénombrer les orignaux dans le sud-ouest du Québec. Naturaliste can. 106: 487-495.

CZAPLEWSKI, R.L. D.M. CROWE, and L.L. MCDONALD. 1983. Sample sizes and confidence intervals for wildlife population ratios. Wildl. Soc. Bull. 11:121-128.

FRANZMANN, A.W., C.C. SCHWARTZ, and R.O. PETERSON. 1980. Moose calf mortality in summer on the Kenai Peninsula, Alaska. J. Wildl. Manage. 44: 764-768.

GASAWAY, W.C., R.O. STEPHENSON, J.L. DAVIS, P.E.K. SHEPHERD, and O.E. BURRIS. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildl. Monogr. 84, 50 pp.



HABER, G.C. 1977. Socio-ecological dynamics of wolves and prey in a subartic ecosystem. Ph.D. Dissertation, University of British Columbia, Vancouver. 786 pp.

HAUGE, T.M., and L.B. KEITH. 1981. Dynamics of moose populations in northeastern Alberta. J. Wildl. Manage. 45: 573-597.

LACHAPELLE, A., F. MESSIER, AND M. CRÊTE. 1984. Importance de l'orignal dans le régime alimentaire des ours noirs du sud-ouest du Québec. Alces 20: 79-94.

MACNAB, J. 1985. Carrying capacity and related slippery shibboleths. Wildl. Soc. Bull. 13: 403-410.

MESSIER, F. 1985a. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Can. J. Zool. 63: 239-245.

MESSIER, F. 1985b. Social oragnization, spatial distribution, and population density of wolves in relation to moose density. Can. J. Zool. 63: 1068-1077.

MESSIER, F., and M. CRÊTE. 1984. Body condition and population regulation by food resources in moose. Oecologial (Berlin) 65: 44-50.

MESSIER, F., and M. CRÊTE. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia (Berlin) 65: 503-512.

STEWART, R.R., E.H. KOWAL, R. BEAULIEU and T.W. ROCK 1985. The impact of black bear removal on moose calf survival in east-central Saskatchewan. Alces 21: 403-418.

WILTON, M.L., D.M. CARLSON, and C.I. McCALL. 1984. Occurence on neonatal cervids in the spring diet of black bear in south central Ontario. Alces 20: 95-106.

YOUNG, B.F., and R.L. RUFF. 1982. Population dynamics and movements of black bears in east central Alberta. J. Wildl. Manage. 46: 845-860.