MOOSE (*ALCES ALCES*) RUTTING PERIOD VARIATIONS

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ABSTRACT: Variations in the timing of mating periods have been observed in many species of wild ungulates. We examined if this reproductive variation, suggested by some authors for moose, could be formally demonstrated. Because it is difficult to get direct evidence of moose mating, we used a series of variables that have the potential to predict the timing of the mating period: vulnerability to hunting (moose killed per party of hunters), visibility (number of moose seen per hunter group) and vocalization rate (based on 3200 questionnaires). This information was collected from 12 Québec (Canada) wildlife reserves over a 6 to 10-year period for the vulnerability to hunting and over 2 years for the other two indicators. To validate these indicators, vaginal and uterine smears of females harvested were analyzed for the presence of spermatozoids. Our results indicate that hunters' success rate and moose vocalization rate can adequately identify pre-copulation period during which animals actively search for a mate. This search stage precedes copulation by a few days. Based on harvest success and vocalization rate it appears that there is little geographical variation in the timing of rutting periods. In all sampled populations, these variables peaked between September 20 and 30. Furthermore, there is no significant correlation between the timing of rutting period and various environmental variables. However, spontaneous calls were significantly correlated with longitude suggesting that the mating period begins a few days later in the eastern part of the province. If the management objective is to minimize the impact of hunting on moose populations, hunting activities should be avoided until the second week of October. This would minimize male hunting vulnerability and would allow female pregnancy before harvest.

RÉSUMÉ: Des variations géographiques de la période du rut ont été observées chez plusieurs espèces d'ongulés sauvages. Nous avons vérifié si une telle variation reproductive, suggérée par quelques auteurs pour l'orignal, pouvait être formellement démontrée. Il est toutefois difficile d'observer directement le comportement reproducteur de cette espèce. Nous avons donc identifié les diverses phases du rut en utilisant des indicateurs tels la vulnérabilité à la chasse (orignaux tués / groupe de chasseurs), la visibilité et le taux de vocalisation des orignaux (nombres vus ou entendus par groupe de chasseurs). Ces informations ont été récoltées dans 12 réserves fauniques du Québec (Canada) pendant une période de 6 à 10 ans pour la vulnérabilité et pendant 2 ans pour les autres indicateurs. Des frottis vaginaux et utérins des femelles récoltées dans la réserve des Laurentides en 1994 ont été examinés afin d'y détecter la présence de spermatozoïdes. Nos résultats montrent que le succès de chasse et le taux de vocalisation détectent adéquatement la phase pré-copulatoire pendant laquelle les orignaux recherchent activement un partenaire. Celle-ci précède de quelques jours la copulation proprement dite. Dans toutes les populations étudiées, le succès de chasse et le taux de vocalisation ont été maximum entre le 20 et le 30 septembre. Il n'y avait pas de corrélation significative entre le pic du rut et diverses variables environnementales. Le taux d'appels spontanés émis par les orignaux était corrélé avec la longitude suggérant un rut décalé de quelques jours dans l'Est du Québec. Il serait nécessaire d'éviter la chasse avant la deuxième semaine d'octobre pour minimiser l'impact de la chasse sur l'orignal. Ceci permettrait de diminuer la vulnérabilité des mâles et favoriserait l'accouplement des femelles avant la chasse.

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Variations in the timing of mating periods (i.e. period during which copulations take place) were observed in wild ungulates, such as some members of the genus *Odocoileus* (Bronson 1989, Sadleir 1969). Many authors (Bronson 1989, Malpaux *et al.* 1989, Markgren 1969, Sadleir 1969, French *et al.* 1960, Edwards and Ritcey 1958) linked this variability to photoperiod and indirectly to latitude. Other environmental factors such as altitude, local climate, habitat and food quality have also been suggested (Schwartz and Hundertmark 1993, Verme and Doepker 1988, Markgren 1969, Sadleir 1969, Peterson 1955) to explain variations in the timing of mating periods. Biological factors such as population density (Peterson 1974), age (Claveau and Courtois 1992), weight, physical condition of reproductive females (Cameron *et al.* 1993), predation pressure (Bergerud 1975) and sex-ratio (Lent 1974) may also play a role. In bighorn sheep (*Ovis* spp.) (Thompson and Turner 1982, Bunnell 1982), rut variation has been linked to maximization of calf survival through a synchronization of the calving period with the spring green-up.

Based on a literature review, Peterson (1974) and Wilton (1992) indicated that there appears to be variations in the timing of mating periods in moose. In Sweden, Markgren (1969) has suggested that the mating season timing may be a function of a climatic gradient. In the province of Québec, Claveau and Courtois (1992) noted that the peak in moose vulnerability to hunting was 4 to 5 days later in the southeastern part of the province relative to the central part, suggesting a geographic variation. Vallée (1976) and Crête (1982) reached the same conclusion based on the sex-ratio of animals harvested.

Contrary to previous studies, a recent literature review (Sigouin 1995) failed to show a significant correlation between timing of the mating period and latitude in moose. This review was based on data from a limited number of populations in which methods varied; consequently, a need to investigate temporal variations in moose mating periods using a standardized approach became apparent.

Because it is difficult to obtain direct evidence of moose copulation, we used three indicators that can reveal the mating period timing: vulnerability to hunting per sex, visibility and vocalization rate (i.e. number of moose killed, seen or heard calling per hunter group). No study has used these indicators in this way and at this scale. These indicators were used to determine the peak of rutting activities of moose in different Québec regions in a standardized approach. For the purpose of this study, the rut includes the pre-copulation period during which obvious behavioural changes take place and the copulation period itself. Variations were related to environmental (latitude, temperature, precipitation) and biological (population density, sex-ratio) factors.

STUDY AREAS

Information was collected from 12 wildlife reserves (hereafter referred to as WR) distributed throughout southern Québec (Canada). The WRs cover most of the province where moose is present (Fig. 1) and use a quota system where the number of hunters, the hunting period and the number of moose killed per group of hunters (3 or 4 hunters) are controlled. This system provides historical data. Hunting seasons are longer in WRs than in other Québec hunting territories, so they cover the major part of expected rutting period (mid-September through mid-October). Inside each WR, an exclusive hunting territory of at least 20 km^2 is given to each group of hunters for a period varying from 4 to 6 days, diminishing interactions among hunting parties.

Southeastern WRs (Chic-Chocs, Matane, Dunière) permit hunting success greater than

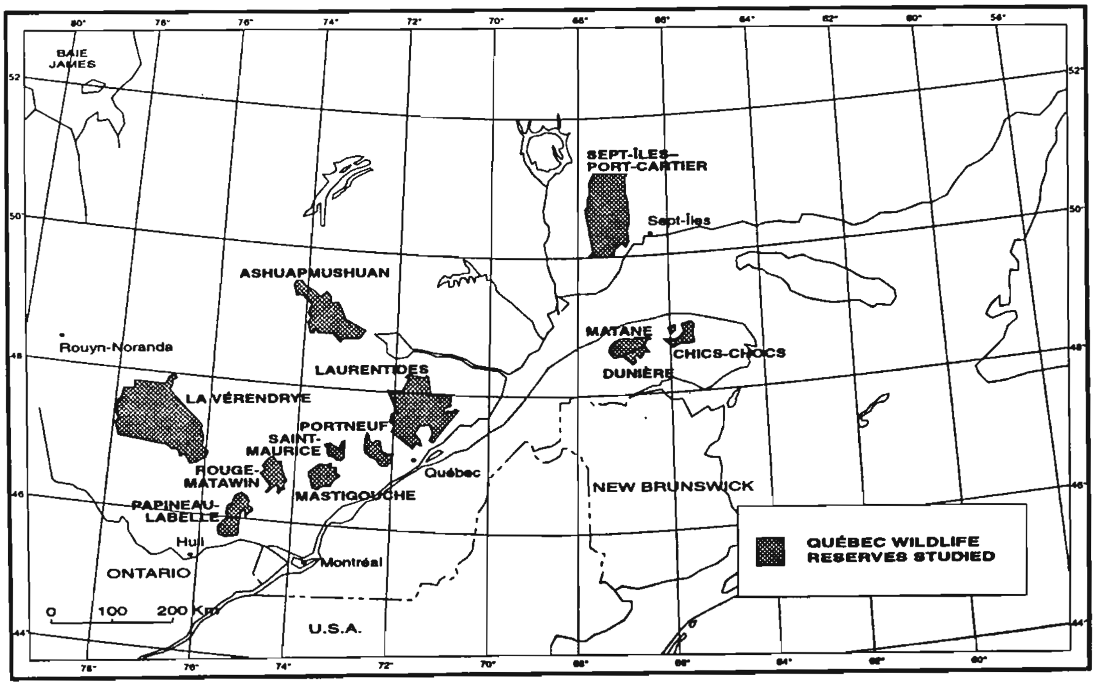

Fig. 1. Québec wildlife reserves sampled for the analysis of moose reproduction period.

75%, reaching nearly 90% in Matane (Table 1) due to very high moose density (>10/10km^2) and the conservative number of hunting parties. Among other WRs, in which density is generally less than 4 moose/10 km^2, only Papineau-Labelle exhibits hunting

Table 1. Population density, hunting success (per party of hunters) and percentage of males in the harvest and in the winter population of wildlife reserves (WRs) considered in this study. The number of hunting parties is also given.

Reserve	Density† (nb/10 km^2)	Hunting success (%)	% males (harvest)	% males† (population)	Hunting parties
Chic Chocs	4.0	76.5	69.8	47	44
Matane	20.3	89.9	65.1	37	89
Dunière	7.3	76.4	78.0	43	50
Sept-Iles/Port-Cartier	0.6	38.6	56.2	42	32
Ashuapmushuan	1.8	25.9	53.2	44	60
Laurentides	2.2	47.1	58.7	35	260
Portneuf	2.5	33.5	60.9	44	95
St-Maurice	1.2	34.0	57.1	49	70
Mastigouche	3.2	43.4	57.3	36	160
Rouge-Matawin	—	46.7	63.8	—	100
Papineau-Labelle	3.9	65.6	63.9	42	84
La Vérendrye	3.5	41.3	67.0	29	391

† Estimated from aerial surveys

success higher than 50%. In all WRs, the percentage of males harvested is over 50% (varying between 53.2 and 78.0%). There is a positive correlation between the percentage of males in the harvest and hunting success ($r = 0.755$, $p < 0.01$). These two factors are also correlated with population density ($r = 0.873$ and $r = 0.836$ respectively, $p < 0.01$). Moose harvest in WRs did not change from 1989 through 1993 (Lamontagne and Gignac 1994), showing that this system is relatively stable over time.

METHODS

Three complementary approaches were used to determine temporal geographic variation in moose rutting periods. First, we used harvest statistics to calculate a hunting success index for each WR. Second, a survey of hunters was conducted to determine the period during which moose were more frequently seen and heard calling. Finally, smears collected from the vaginal and uterine mucosae of females harvested in one WR (Laurentides) were examined to cross-validate harvest statistics and survey results. This verification was also possible for another WR (Matane) using previously published results (Claveau and Courtois 1992).

Hunting success

The Québec Ministry of Environment and Wildlife provided harvest statistics that were used to obtain hunting success for males and females. Data existed for a 6 to 10-year period, depending on the WR. Hunting success was analyzed by 5-day periods to minimize daily climatic variation effect. These periods were standardised to simplify comparisons between WRs. Periods began the 3rd, 8th, 13th, 18th, 23rd and 28th of September and October. For each period of 5 days within each year and for each WR, we calculated hunting success deviation relative to the mean hunting success in order to identify peak vulnerability. Data were pooled across years and the mean annual deviation and the standard errors were calculated within each time period.

Visibility and vocalizations

Over two hunting seasons (1993 and 1994), 3200 questionnaires were given to hunters (one per hunting party) at the beginning of their hunting expedition. They were asked to record the number of moose observed, the number of vocalizations heard and the number of answers to their own calls. Hunting success for each 5-day period was also considered. The questionnaire response rate was 84%.

Vaginal and uterine smears

Females shot in Laurentides WR during the hunting season of 1993 were examined for the presence of spermatozoids in their genital tract. No samples were available in 1994 because regulations precluded adult female harvest. Hunters had to bring back the entire female genitalia including vulva, vagina, uterus and ovaries (all in one piece). An information pamphlet was given to each group of hunters and verbal explanations were given at the beginning of their hunting expedition. Shortly after death (i.e. within 36 hours), the genitalia was opened, beginning by the vulva and exposing the inner wall of the vagina and the uterus. An internal mucosae sample from each of these structures was deposited on a slide and dried at air temperature. To detect spermatozoid presence, each sample was examined using a microscope at 400X enlargement.

Environmental variables

Environmental variables were: beginning, end and length of the growing season, latitude, longitude, snowfall, total precipitation, and mean temperature. These data were based on a 30-year average from weather stations (Environment Canada 1982) located in close proximity to each WR. The growing season length was defined as the number of days from the last spring to the first fall occurrence of 0°C temperature or below (Thompson and Turner 1982).

Data analysis

Spearman's rank correlations were calculated between the date of the maximum value of each indicator (vulnerability, visibility and vocalizations) and the environmental variables considered (see above). The significance level was conservatively set at 0.01 to minimize type I error generated by the large number of correlations conducted.

RESULTS

Hunting success

There was no significant correlation ($p < 0.01$) between the peak date of hunting success for males or females and environmental variables considered (Table 2). Moreover, correlation coefficients were weak except for latitude. In all but one WR (Dunière; October 5), hunting success for males peaked between September 20 and 30 inclusively (Fig. 2) suggesting that males are more vulnerable to hunting during the last two weeks of September. Overall hunting success was lower for females than for males ($t = -3.069$, $p = 0.015$), although it was often higher at the beginning or at the end of the hunting season. During these periods, in many WRs, hunting success for females was equivalent or even superior relative to males (Fig. 2).

Visibility

Dates corresponding to the maximum number of males and females seen by hunters were not significantly correlated with any environmental variable considered (Table 2). In 9 of the 12 WRs, the number of males seen reached a maximum value during the periods of September 20 and 25 (Fig. 3). But for many WRs, no clearly defined peak was observed. As was the case for hunting success, females were seen more often prior to September 20 and in October.

Table 2. Correlation coefficients (Spearman) between the date corresponding to the maximal value of each indicator (hunting success, visibility and vocalizations) and environmental variables considered (n = 12).

Environmental variables	Success		Visibility		Vocalizations	
	Males	Females	Males	Females	Spontaneous	Answers
Beginning of the growing season	0.372	-0.118	0.666	0.518	0.110	0.087
End of the growing season	-0.272	0.124	-0.605	-0.623	-0.161	-0.127
Length of the growing season	-0.525	-0.024	-0.576	-0.504	-0.013	0.038
Latitude	0.250	0.524	0.433	0.188	0.344	0.643
Longitude	-0.213	-0.289	-0.327	-0.212	-0.489	-0.760*
Snowfall	-0.006	-0.180	0.097	0.039	0.248	0.573
Total precipitation	-0.069	-0.271	-0.036	0.150	0.200	0.455
Mean temperature	-0.330	-0.191	-0.698	-0.456	-0.267	-0.538
Density	-0.164	-0.306	-0.060	0.194	0.338	0.220
Hunting success	-0.050	-0.459	0.286	0.191	0.259	0.233
% males (harvest)	-0.138	-0.267	-0.102	0.227	0.522	0.177
% males (population)	0.360	0.408	-0.037	-0.453	-0.019	0.063

* $p < 0.01$

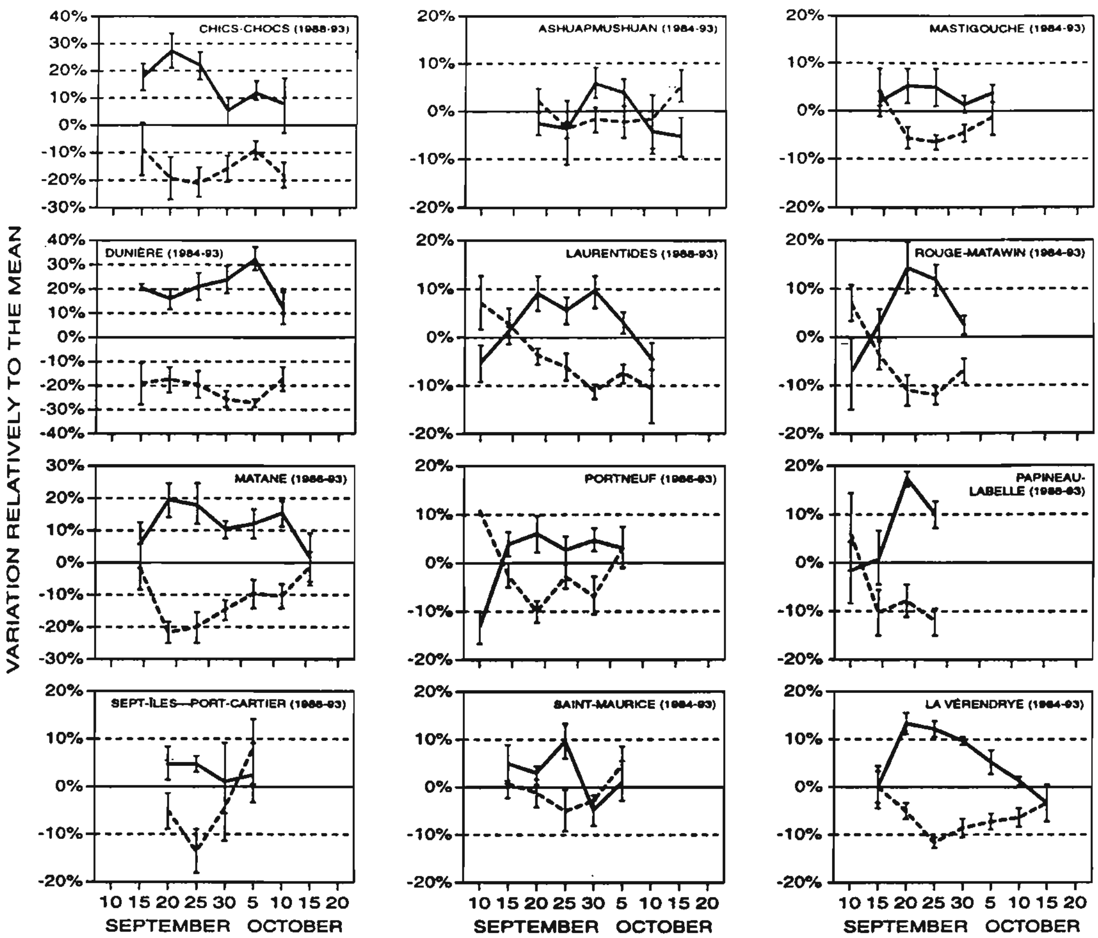

Fig. 2. Temporal variability in hunting success of males (——) and females (---) in 12 Québec wildlife reserves. Based on an average of 1025 hunting parties per reserve (range: 189-3909).

Vocalizations

The maximum number of spontaneous calls was recorded between September 20 and 30 for 11 of the 12 WRs investigated (Fig. 4). For answers to hunters, maximum values were also recorded between September 20 and 30 (except for Sept-Iles/Port-Cartier and Rouge-Matawin). Peak of answers was September 20 in the western part of the province, while it was later (September 25) in eastern WRs (Chic Chocs, Matane and Dunière). The timing of the answers was negatively correlated with longitude, indicating a delay in the eastern WRs.

Vaginal and uterine smears

Vaginal and uterine smears were taken from 38 adult females killed in Laurentides reserve between September 13 and October 12, 1993. The first positive smear was recorded on September 30 (Table 3) despite the fact that 22 adult females were analyzed prior to September 30. Two other females were found positive on October 10 and another one on October 11. The low number of females examined between September 30 and October 10 may explain the absence of positive smears during that period.

DISCUSSION

Many behavioural changes occur in

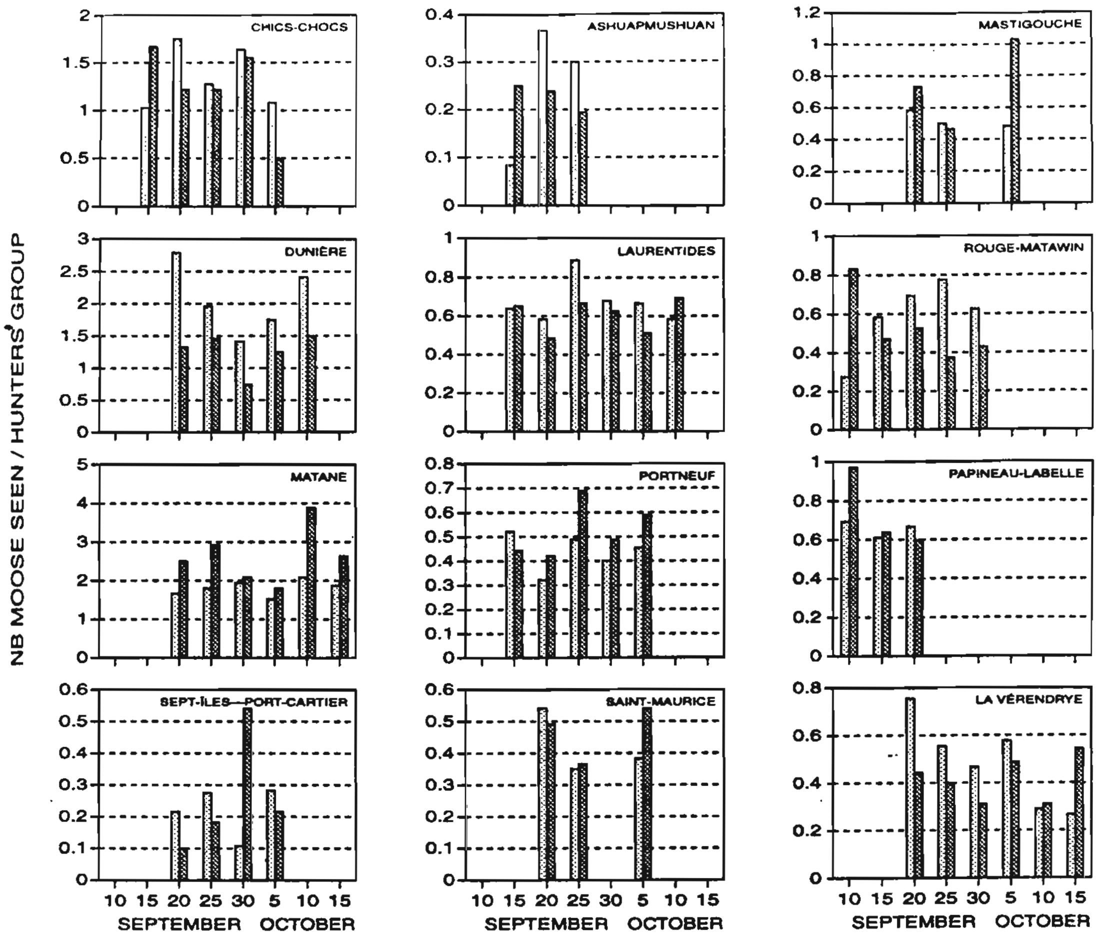

Fig. 3. Temporal variability in the number of males (□) and females (■) seen by hunters in 12 Québec wildlife reserves. Based on an average of 206 hunting parties per reserve (range: 62-642).

Table 3. Number of vaginal and uterine smears in Laurentides WR for each hunting period in 1993 for females ≥ 1.5 year.

Period (median date)	Number of smears	Age of females $\overline{X} \pm SE$	Number of positive smears
15 September	4	1.8 ± 0.3	0
20 September	7	3.8 ± 0.7	0
25 September	9	5.1 ± 1.7	0
30 September	6	4.9 ± 1.3	1
5 October	5	4.1 ± 2.2	0
10 October	7	3.7 ± 1.1	3
Total	38	4.1 ± 0.6	4

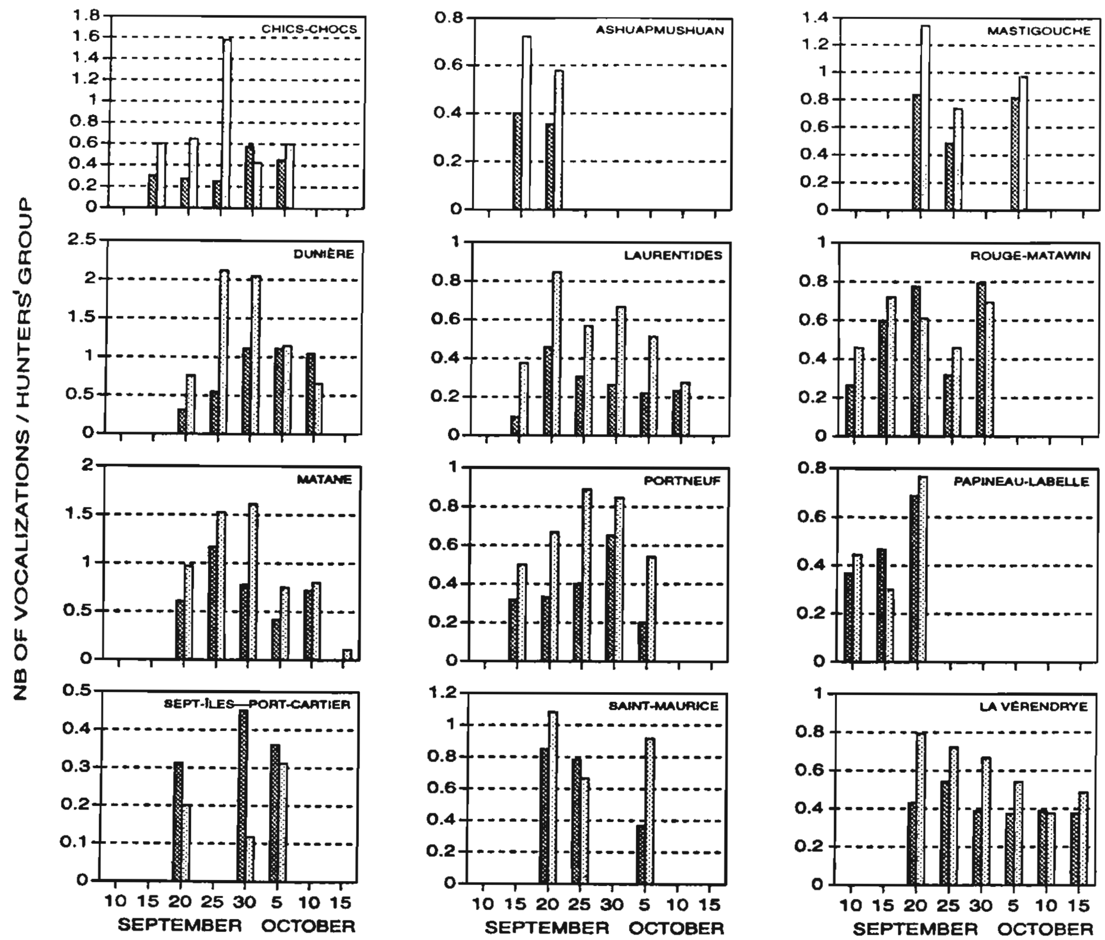

Fig. 4. Temporal variability in the number of spontaneous calls (□) and answers to hunters (■) in 12 Québec wildlife reserves. Based on an average of 206 hunting parties per reserve (range: 62-642).

moose prior to and during the rutting period. In Alaska, the reproduction period of moose can be divided into three distinct phases (Miquelle 1991). First, velvet is shed from antlers and bulls aggregate; secondly, bulls defend and court females; lastly, copulations take place. Although the rut may be different in Alaska, as moose may aggregate to reproduce (Miquelle 1991), distinct phases must exist in Québec and may be detected by our analysis. During the rut, males are more vulnerable to hunting (Crête *et al.* 1981, Bangs *et al.* 1984, Dussault and Huot 1986, Ritcey 1974) because they are more mobile (Courtois *et al.* 1993, Labonté *et al.* 1993, Mytton and Keith 1981, Roussel *et al.* 1975, Lent 1974). This behaviour has been linked to the search for females and often appears in response to her call (deVos *et al.* 1967). Because moose have large home-ranges (Courtois *et al.* 1993, Labonté *et al.* 1993) and as they often live at relatively low densities (Courtois 1991, Crête 1989) vocalization makes it easier to search for an individual of the opposite sex. It is well known that hunters mimic this behaviour to lure males and increase their hunting success. Dussault and Huot (1986) have shown a relationship between the vocalization rate peak and hunting success. The indicators considered (harvest success, visibility and vocalizations) likely detected the pre-copulation (search stage)

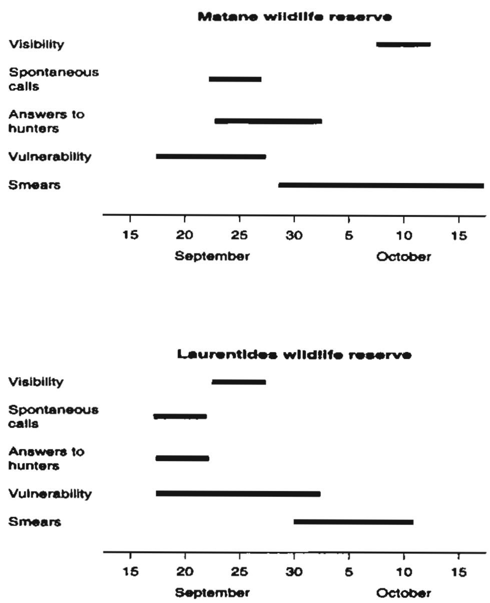

Fig. 5. Peak rutting activities based on moose visibility, calls and answers compared to smears positiveness.

period, which is the period when males search for and court females.

Validation of the various indicators

Our results show that harvest success and vocalization rate are the best indicators of the timing of the pre-copulation period. This is confirmed, although based on a limited sample size, by vaginal and uterine smears. This technique proved to be appropriate to determine the beginning of the mating period but do not allow precise determination of the peak copulation period because spermatozoids can be detected in the genital tract for up to 72 hours (Claveau and Courtois 1992).

Moose visibility did not appear to be an adequate indicator of the timing of reproductive events. For Laurentides WR, this indicator provided results similar to those of the other two indicators. However, at Matane WR, the visibility peak occurred during the mating period (i.e. when the majority of copulations took place) (Fig. 5). Furthermore, there is no well defined peak in moose visibility for most WRs (Fig. 3). Moose visibility may occur over a longer period of time thus limiting its use as an indicator of reproductive timing.

Timing of rutting periods

Based on vaginal and uterine smears collected at Matane WR from 264 females over a 9-year period, Claveau and Courtois (1992) found that copulation generally began between October 2 and 5 (range: September 28 - October 7). The same tendency was observed in Laurentides WR (i.e. copulations began September 30; Fig. 5) but only one sampling year was available in that specific case. Spontaneous calls and answers to the calls, as well as harvest success for males, peaked shortly before the copulation period began. These indicators appear to be associated with the search stage of the rutting period. Increased hunting vulnerability appears to be clearly linked to behavioural modifications during the rut. Although, there were twice as many females (Courtois 1991), male harvest success was often higher during the search stage of the rutting period. Outside this period, harvest success becomes equal between the two sexes.

Harvest success and vocalization rate suggest that there is little geographic variation in the timing of rutting periods throughout the province of Québec. In all WRs, these indicators peaked between September 20 and 30 indicating that pre-copulation activities were maximum during that period. This corresponds to the finding of Dussault and Huot (1986) in Laurentides WR. In Sept-Iles—Port-Cartier, Portneuf, and Mastigouche WRs, the harvest success peak was not well defined. This does not seem linked to sample size. For example, Mastigouche is one of the WRs where the greatest number of moose was killed. Consequently, we can speculate that some biological factors may have caused the maximum vulnerability period to be longer in these WRs.

Answers to hunters seem to occur a few days later in the southeastern part of the province (e.g. Chic-Chocs, Dunière, and Matane WRs; Fig. 4). This is supported by significant correlation between spontaneous calls and longitude. These results support the suggestion made by several authors (Claveau and Courtois 1992; Crête 1982; Vallée 1976) that the reproductive season may be occurring a few days later in eastern Québec. If such variation exists, we cannot speculate about its cause because no environmental factor was linked to the peak of vocalizations or to the harvest success. Moreover, one must consider that this asynchrony is rather subtle.

Our analysis and previous works (Dussault and Huot 1986, Claveau and Courtois 1992) show that, in Québec, moose rutting activities begin between the end of August and mid-September. Then, males actively search for a mate between September 20 and 30 while most copulations occur during the first week of October. The second peak of copulation activities should take place 24-25 days later (Schwartz and Hundertmark 1993) around October 20 to 25.

Management implications

From a management perspective, it is crucial to know the peak rutting period to determine when the hunting season should open. For example, males vulnerability to hunting will be reduced if hunting season begins after the main rutting period. Hunting of dominant males may adversely affect the gene pool of subsequent generations (Wilton 1992), particularily where hunting rate is high enough to substantially lower moose densities. Females may also be more vulnerable during the rut because they also increase their movements during this period (Claveau and Courtois 1992, Labonté *et al.* 1993).

In Québec, males were particularly vulnerable to hunting from September 20 to 30. Considering that copulation begins in the last part of September, and that males follow females for up to 5 days (Bubenik 1987), we need to avoid hunting during this period if we want a maximum number of females to copulate. As underlined by Wilton (1992), moose hunting season should not be too early. In Ontario, Gollat *et al.* (1981) used movements and vocalization indicators to determine that the peak of the rut was in the last two weeks of September and in the first week of October. To limit the influence of hunting during the period when males are most vulnerable, they suggested moving the start of the hunting season to the end of October.

Rutting activities appear to take place over a two-month period (Claveau and Courtois 1992). However, many behaviour changes occur during this period; some of them are important from a management perspective. Male vulnerability peaked at the end of September while that of females is higher in October. If the management objective is to favor a balanced sex-ratio, hunting could take place as early as the first week of October. However, if managers want to maximize female pregnancy, hunting activities should be avoided at least until the second week of October. In addition, the lack of a marked geographical variability in the moose reproductive period in Québec suggests that a fixed hunting season over the entire province could be acceptable. But, it would be conservative to begin the hunting season a few days later in southeastern Québec.

Our results should be cautiously applied to other hunting territories in the province of Québec. Exploitation rate is markedly higher outside wildlife reserves (Courtois *et al.* 1994), and as a result, mean age of individuals decreases (Caughley 1974; Courtois and Lamontagne 1990). In many ungulate species, young individuals delay calving or mating (Bailey and Bangs 1980, Bubenik and Timmermann 1983, Claveau and Courtois 1992, Clutton-Brock *et al.* 1992, Saether and Heim 1993) increasing the duration of the mating period. In highly exploited areas, this could extend the vulnerability period.

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