GEOGRAPHICAL VARIATION IN THE MATING AND CALVING PERIODS OF MOOSE

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ABSTRACT: In some ungulates, variations in the timing of mating and calving periods are related to environmental conditions. It has been suggested that such an adjustment of the timing of reproductive events to local conditions would maximise calf survival as the calf benefits from abundant high quality forage during the early stages of lactation. Published data were analysed to assess the existence of temporal variations in reproductive events for moose (*Alces alces*). Dates corresponding to mating (n = 19) and calving (n = 18) periods (median, beginning, end, and duration) were correlated to latitude, longitude and climatic parameters (temperature, precipitation, timing of the growing season) obtained from weather stations. Most mating occurred over a 15-day period, from 23 September to 8 October. Most births were recorded over 19 days, between 19 May and 8 June. The only significant correlation found ($P < 0.01$) relates the beginning of the mating period to mean total snowfall. Results suggest that variations in the timing of the reproductive events among moose populations are weak and independent from the influence of environmental conditions. Comparisons with other species suggest that the low variability in environmental conditions encountered by the populations studied could, in part, explain this finding.

RÉSUMÉ: On note, chez certains ongulés, une synchronisation temporelle entre les périodes de fécondation et de mise bas et certaines conditions environnementales. Cet ajustement aux conditions locales permettrait de maximiser la survie des nouveau-nés en ajustant la naissance à l'abondance d'une nourriture de qualité. Les données publiées ont été utilisées pour vérifier l'existence d'une telle relation chez l'orignal (*Alces alces*). Les caractéristiques temporelles (date centrale, date du début, date de la fin et durée) des périodes de fécondation (n = 19) et de mise bas (n = 18) des différentes populations ont été corrélées à la latitude, à la longitude et à une série de données climatiques (température, précipitations, date du début, de la fin, et durée de la saison de croissance des végétaux). Dans les études consultées, la majorité des fécondations survient entre le 23 septembre et le 8 octobre, soit une période de 15 jours. La majorité des mises bas s'étale sur 19 jours, soit entre le 19 mai et le 8 juin. La seule corrélation significative ($P < 0,01$) notée relie le début de la période de fécondation et les précipitations nivales. Chez l'orignal, les variations des périodes de fécondation et de mise bas semblent de faible amplitude et indépendantes des conditions environnementales. La comparaison avec d'autres espèces suggère que la faible variabilité des conditions environnementales rencontrées par les différentes populations d'orignaux considérées pourrait expliquer cette situation.

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In ungulates living in seasonal environments, there is generally a certain synchronization of the mating and calving periods for individuals within the same population. This phenomenon has been observed in many species such as bison (*Bison bison*), caribou (*Rangifer tarandus*), deer (*Odocoileus* spp), bighorn sheep (*Ovis* spp) and moose (*Alces alces*) (Edwards and Ritcey 1958, Bergerud 1975, Bunnell 1982, Thompson and Turner 1982, Bronson 1989, Skogland 1989, Schwartz *et al.* 1990, Berger 1992). In Odocoileus, Bronson (1989) points out that south of 30° latitude reproduction takes place at any given time during the year. On the other hand, north of this limit there is a definite synchronous reproductive season. It has been argued that this synchronization maximizes the survival of neonates (Sadleir 1969, Festa-Bianchet 1988, Schwartz *et al.* 1990). Some authors have suggested that this synchronization minimises the risk of predation (Bergerud 1975, Rutberg 1987, Berger 1992). However, the most frequently cited reason is the periodicity in food availability caused by the short growing season, particularly in cold temperate regions (Festa-Bianchet 1988, Rutberg 1987, Skogland 1989). It is important that the calving period occur in a period offering high quality forage to allow maximum growth of calves prior to winter, thereby increasing their survival rate (Thompson 1980, Meech *et al.* 1987, Crête and Courtois 1996). Moreover, lactation by increasing energy demand on the dam, necessitates access to an adequate food supply to meet both female and neonate requirements (Festa-Bianchet 1988). The highest quality of the food supply is found at the beginning of the growing season (Albon and Langvatn 1992, Ouellet *et al.* 1994). Consequently, it may be advantageous if the calving period coincides with the beginning of the growing season. The initiation and the duration of the vegetation growing season depend on several climatic factors (temperature, precipitation) and the photoperiod (Bronson 1989). The photoperiod could induce reproduction in Nordic environments (Sadleir 1969, Deveson *et al.* 1992, O'Callaghan *et al.* 1992). Moreover, the photoperiod is correlated to the latitude, that is, an increase in latitude generally implies a delayed and shorter growing season (Thompson and Turner 1982), due to less degrees-day in spite of a longer day length in summer (J. Cihlar, Centre Canadien de Télédétection, pers. comm.).

The relation between the timing of reproduction and environmental factors has been demonstrated at both the specific and interspecific levels. For example, in caribou, Skogland (1989) found a significant correlation between the start of the calving period and the start of the growing season as well as between the synchrony of births and the length of the snow-free season. In bighorn sheep, Bunnell (1982) as well as Thompson and Turner (1982) reported a significant correlation between the lambing period and latitude as well as with some other climatic variables such as mean annual temperature, total precipitation and total snowfall. Altitude is also a factor that can potentially determine seasonal variation in reproductive strategies (Bronson 1989) by acting, in many ways, similarly to latitude. As a matter of fact, lower temperatures prevailing at higher altitudes affect the timing of snow melting and thus, the length of the growing season (Sadleir 1969). Bunnell (1980) also suggested that recruitment was correlated to the precipitation in April and May, at which time, low temperatures reduced the survival rate of the offspring. To our knowledge, no other ungulate has been similarly studied to detect such a temporal adjustment of the mating and calving periods to local environmental conditions even though, some authors have suggested the existence of such a relationship in moose (Sadleir 1969, Markgren 1969, Claveau and Courtois 1992).

The objective of this study was to examine the variation in the mating and the calving periods of moose from the published literature. We hypothesize that the reproduction period of moose is a function of latitude or other climatic variables (i.e., precipitation and temperature).

METHODS

Dates of the mating (n = 19) and the calving periods (n = 18) of different North American and European moose populations were obtained from the literature. In North America, data were collected from study areas in Canada and the United States (Alaska principally). In Europe, data from Sweden and the USSR were used. When dates were given in terms of weeks, the month was divided into four weeks and the first day of each week was retained. Also, when authors gave the beginning, the end or half of a month as reference, periods were considered to begin or finish respectively on the first, the last or 15th day of the month. When the beginning and the end were provided, we calculated a central date ([beginning + end]/2). As the majority of the reproductive activity takes place at the beginning of the reproduction period, it is unlikely that dates of mating and calving period follow a normal distribution (Festa-Bianchet 1988, Ballard *et al.* 1991). Thus, the central date does not necessarily correspond to the median. All calendar dates where converted into Julian days for analysis purposes.

Geographical variables (latitude, longitude) were obtained from publications or through an atlas describing the location of the study areas (Tables 1 and 2). Climatic data, compiled over a 30-year period (temperature, precipitation, date of the beginning, the end, and the duration of the growing season) were obtained from Canadian, American and world Environmental Services, (United States National Oceanic and Atmospheric Administration 1968, 1980; Environment Canada, Service of the Atmospheric Environment 1982; Müller 1982). The growing season was considered to be the period without frost, that is the period between the last frost in spring and the first frost in autumn (Thompson and Turner 1982).

We correlated the dates (i.e., central, beginning, end) and length of the mating and calving periods to climatic data in order to verify if there was a relationship between these variables. The following hypotheses were evaluated against the null hypothesis of no correlation between the studied parameters and the features of the mating and calving periods.

H1: Mating and calving period begin later and end earlier at more northern latitudes.

H2: Mating and calving periods features are correlated to the growing season parameters.

H3: Mating and calving periods begin later and end earlier when mean annual temperature decreases.

H4: Mating and calving periods begin later and end earlier when snowfall increases.

Hypothesis H3 and hypothesis H4 are intimately related to H2. Indeed, lower temperatures and important snowfalls should reduce the length of the growing season and may affect calf survival (Bunnell 1980).

Normality was assessed graphically and by testing skewness and kurtosis (Zar 1984). Spearman correlations ($p = 0.01$) were used as data were not normally distributed. A 0.01 probability level was retained to minimize the type I error due to the great number of correlations undertaken.

RESULTS

No parameter of the mating period (i.e., central date, beginning, end, and duration) was significantly correlated to the latitude or to the features (beginning, end, duration) of the vegetation growing season (Table 3). Nevertheless, the beginning of the mating period was correlated to the mean total snowfall ($r = 0.915$; $p < 0.01$), which was negatively correlated with the end of the growing season ($r = -0.759$; $p < 0.01$). So, more snowfall is related to an earlier end of the growing season and a delayed beginning of the mating period. For all studies, the majority of mating occurs between 23 September and 8 October, a period of 15 days between 43° to 67° N latitude (Fig. 1).

On the other hand, no significant correlation was observed between the environmental variables considered for the calving period (i.e., central date, beginning, end, and duration) (Table 4). Similarly, for all studies, the calving period lasts from 19 May to 8

Table 1. Databases from the litterature used to study the relationship between environmental variables and the mating period of moose.

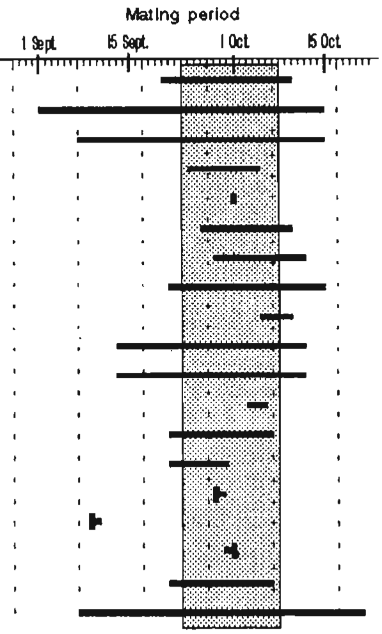
Source	Study area	Latitude	Longitude	Growing season			Precipitation (cm)		Mean temperature °C
				Beginning	End	Length	Snow	Rain	
Aitken and Child (1992)	British Columbia	53	125	182	232	49	187	34	2.0
Altman (1959)	Wyoming	43	108	142	260	118			7.8
Claveau and Courtois (1992)	Québec	49	67	171	234	62	354	68	1.2
Crichton (1992)	Manitoba	55	98	151	256	104	148	32	-2.2
Dodds (1958)	Newfoundland	48	57	164	246	81	163	79	3.9
Edward and Ritcey (1958)	British Columbia	52	120	172	214	41	211	36	3.7
Hauge and Keith (1981)	Alberta	57	112	158	243	84	164	33	-0.2
Knorre (1959) in Lent (1974)	USSR	68	-60[a]						-3.9
Markgren (1969)	Sweden	61	-16[a]						6.6
Miquelle (1990)	Alaska	64	150	156	239	83	272		0.7
Miquelle (1991)	Alaska	64	150	156	239	83	272		0.7
Peek (1962)	Montana	45	112	151	250	99	84		6.4
Schladweiler and Stevens (1973)	Montana	47	110	136	268	132			
Schwartz and Hundertmark (1993)	Alaska	63	150	156	239	83	272		0.7
Van Ballengerghe and Miquelle (1993)	Alaska	64	150	140	244	104	174		-3.4
Yazan (1961) in Lent (1974)	USSR	68	-60[a]						-3.9

[a] A negative longitude indicates a location eastward from Greenwich

Table 2. Databases from the litterature used to study the relationship between environmental variables and the calving period of moose.

Source	Study area	Latitude	Longitude	Growing season			Precipitation (cm)		Mean temperature °C
				Beginning	End	Length	Snow	Rain	
Addison *et al.* (1993)	Ontario	45	79	144	264	119	290	64	3.9
Albright and Keith (1987)	Newfoundland	48	58	141	281	139	411	72	5.1
Altman (1959)	Wyoming	43	108	142	260	118			7.8
Bailey and Bangs (1980)	Alaska	61	150	137	257	130	179		2.1
Ballard *et al.* (1991)	Alaska	62	150	156	239	83	272		0.7
Ballard *et al.* (1981)	Alaska	63	145	136	250	114	104		
Cederlund *et al.* (1987)	Sweden	61	-15[a]						6.2
Franzmann *et al.* (1980)	Alaska	61	151	150	240	90			
Gasaway *et al.* (1983)	Alaska	64	149	163	228	65	210		-2.6
Langley and Pletscher (1994)	British Columbia	49	113	144	256	111	229	32	4.8
Larsen *et al.* (1989)	Yukon	61	135	159	242	82	137	15	-1.2
LeResche (1968)	Alaska	63	150	156	239	83	272		0.7
Markgren (1969)	Sweden	61	-16[a]						6.6
MEF (unpublished)	Québec	47	76	152	256	103	302	75	3.4
Peek (1962)	Montana	45	112	151	250	99	84		6.4
Schwartz and	Alaska	63	150	156	239	83	272		0.7
Stringham (1974)	Alaska	58	155	120	282	162	227		4.8
Van Ballenberghe (1979)	Alaska	61	150	137	257	130	179		2.1

[a] A negative longitude indicates a location eastward from Greenwich



Source	Study area	Period	Latitude
Egorov (1965) in Peterson (1974)	USSR	Peak	---
Knorre (1959) in Lent (1974)	USSR	All	67.5
Yazan (1961) in Lent (1974)	USSR	All	67.5
Van Ballenberghe & Miquelle (1993)	Alaska	All	64
Miquelle (1990)	Alaska	Median	63.5
Miquelle (1991)	Alaska	All	63.5
Schwartz & Hundertmark (1993)	Alaska	All	63
Rausch (1959) in Lent (1974)	Alaska	All	---
Markgren (1969)	Sweden	Peak	61
Crichton (1992)	Manitoba	All	50-60
Hauge & Keith (1981)	Alberta	All	57
Aitken & Child (1992)	British Colombia	Mean	53
Edward & Ritcey (1958)	British Colombia	All	52
Simkin (1974)	Ontario	Peak	---
Claveau & Courtois (1992)	Québec	Beginning	48.5
Dodds (1958)	Newfoundland	Beginning	48
Schladweiler & Stevens (1973)	Montana	End (92%)	47
Peek (1962)	Montana	Peak	45
Altman (1959)	Wyoming	All	43

Fig. 1. Mating period for moose populations in relation to latitude. The hatched zone represents the period where all central dates are included. The "period" field indicates if the mating period is complete or partial (├ = beginning, ┤ = end of the period).

Table 3. Spearman rank correlation coefficients between date (central, beginning, end) of the mating period of moose and environmental variables. (N)

	Mating period			
Variable	Central date	Beginning date	End date	Length
Growing season				
Beginning	0.185	0.190	0.295	0.110
	(9)	(9)	(8)	(7)
End	-0.504	-0.747	0.000	0.495
	(9)	(9)	(8)	(7)
Length	-0.434	-0.441	-0.049	0.417
	(9)	(9)	(8)	(7)
Latitude	-0.177	-0.103	0.173	-0.064
	(12)	(11)	(10)	(9)
Precipitation				
Snowfall	0.727	0.915*	-0.216	-0.627
	(8)	(8)	(6)	(6)
Total	0.510	0.602	-0.421	-0.498
	(12)	(11)	(9)	(9)
Mean temperature	0.573	0.221	-0.094	-0.140
	(12)	(11)	(9)	(9)

* p < 0.01

Table 4. Spearman rank correlation coefficients[1] between date (central, beginning, end) of the calving period of moose and environmental variables. (N)

Variable	Mating period			
	Central date	Beginning date	End date	Length
Growing season				
Beginning	-0.142	-0.105	-0.365	-0.059
	(13)	(11)	(10)	(9)
End	-0.160	-0.369	0.357	0.445
	(13)	(11)	(10)	(9)
Length	-0.084	-0.114	0.315	0.318
	(13)	(11)	(10)	(9)
Latitude	0.316	0.383	-0.197	-0.308
	(15)	(11)	(10)	(9)
Precipitation				
Snowfall	-0.730	-0.750	-0.577	0.323
	(11)	(10)	(9)	(8)
Total	-0.493	-0.342	-0.503	0.025
	(14)	(11)	(10)	(9)
Mean temperature	-0.289	-0.256	0.158	0.168
	(13)	(10)	(9)	(8)

[1]All correlations are non-significant at $P < 0.01$

June, a period of 19 days (Fig. 2), for those populations between 43° to 64° N latitude.

DISCUSSION

This review illustrates variability in the mating and calving periods of moose over its circumpolar distribution. This variability is however weak in amplitude and, contrary to our hypotheses, the timing of both periods is not correlated to latitude nor the features of the growing season. The data indicate rather that the beginning of the mating period is seemingly correlated to the mean total snowfall (which is correlated with the end of the growing season). One could then expect that important total snowfall would shorten the length of the growing season and delay the beginning of the mating period. However, no significant correlation was found between total snowfall and either of the other features of the mating period and the parameters of the calving period. Therefore, we suspect this relationship to be fortuitous.

No other comparable study has been conducted for moose so far. But some studies on bighorn sheep have demonstrated major variations in the features of the lambing period that were correlated with latitude and some parameters of the growing season (Bunnell 1982, Thompson and Turner 1982). However, no correlation with latitude was found ($p > 0.01$) when southern and Nordic populations of bighorn sheep were considered separately. The threshold separating these populations is near 38° N latitude, where alpine habitat is characteristic to the north and desert habitat dominates the south. Besides, the span of environmental conditions met by the different bighorn sheep populations is far more important than for moose populations considered in this study. For example, the range of values corresponding

Source	Study area	Period	Latitude
Gasaway et al. (1983)	Alaska	All	64
Le Resche (1968)	Alaska	End (84%)	63
Schwartz & Hundertmark (1993)	Alaska	All	63
Ballard et al. (1981)	Alaska	All	63
Ballard et al. (1991)	Alaska	Peak	62
Bailey & Bangs (1980)	Alaska	Peak	61
Van Ballenberghe (1979)	Alaska	All	61
Larsen et al. (1989)	Yukon	All	61
Markgren (1969)	Sweden	Peak	61
Cederlund et al. (1987)	Sweden	Peak	61
Franzmann et al. (1980)	Alaska	Peak	60.5
Stringham (1974)	Alaska	All	58
Langley et Pletscher (1994)	British Colombia	Beginning	49
Albright & Keith (1987)	Newfoundland	2 dates	48
MEF (unpublished)	Québec	All	47
Addison et al. (1993)	Ontario	Beginning	45.5
Peek (1962)	Montana	All	45
Altman (1959)	Wyoming	All	43

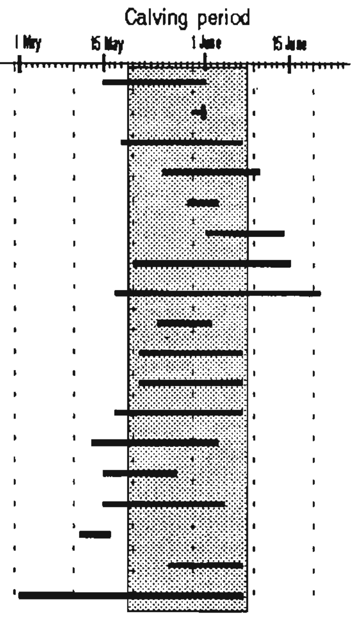


Figure 2. Calving period for moose populations in relation to latitude. The hatched zone represents the period where all central dates are included. The (period(fie(| = peak, | = end of the period).

to the beginning of the growing season is 45 days in moose as compared to 155 days in bighorn sheep. The greatest variability in environmental conditions found in bighorn sheep is partly a function of its wide latitudinal distribution but also of its important altitudinal range (0 to 4268 m, Thompson and Turner 1982). The moose is a boreal forest species and is present only in the northern part of North America (Coady 1982). The most southerly population considered in our study was situated at 43° N and generally at less than 800 m, which is far from the range of environmental conditions encountered by bighorn sheep and may partly explain why no relation was found.

Our study suggests that temporal variations in mating and calving periods are weak amongst different moose populations. This is in keeping with observations made by other authors who report little variability in the reproductive events within (Edwards and Ritcey 1958, Lent 1974) or between (Wilton 1992) study sites. This also supports the observations of Sigouin *et al.* (1995) who reported a variation of only a few days in the timing of mating events for moose in Québec.

To conduct this analysis we used data from various studies which did not address as their main objective the timing of either the mating or calving periods. Consequently, methods used to determine these periods varied greatly from one study to the next, masking potential small differences. Furthermore, the number of populations considered was limited. To more fully demonstrate the temporal variations in mating and calving periods and the adaptive value of this relationship, it would be necessary (1) to cover the total distribution of the species (2) to use a standardized approach of study to cover the total distribution of the species, and (3) since it is difficult to observe moose during the rut, it would be desirable to use one or more indices associated with the reproductive behavior (e.g. moose call, De Vos *et al.* 1967). Such an approach has been successfully used in moose on a portion of its distribution area (Sigouin *et al.* 1995). It is obviously not possible to conduct this type of analysis from the published literature. Moreover, it would be desirable to consider biological factors (density and sex-ratio: Sadleir 1969, Lent 1974, Crête *et al.* 1981; nutritional conditions: Schwartz and Hundertmark 1993) liable to influence the synchronization of the reproduction period in moose as they may act as confounding factors, but such data remain scarce.

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