TEMPORAL PATTERNS IN SASKATCHEWAN MOOSE POPULATIONS, 1955 - 1988

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ABSTRACT: Thirty-four years (1955-1988) of moose aerial transect trend survey data were evaluated to determine long term population trends and the presence and duration of any cycles within 4 broad regions within the commercial forest zone of Saskatchewan. Inspection of the datasets combined with analysis of 5- and 9- year moving averages resulted in the identification of distinct 9-11 year synchronous cycles in density estimates for each of the 4 areas. The data were suggestive of populations which were high at the turn of each decade and low at mid-decade. These cycles occurred regardless of the overall population trends for each area. Futher evaluation of data on hunter effort failed to establish any simple link between hunter effort and the observed cycles.

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From analysis of long term trend aerial survey data, we report on evidence which indicates the possibility of regular cycling in moose (*Alces alces andersoni*) populations in Saskatchewan. The major difficulty in attempting to assess cycling in long lived mammals is the lack of long-term population data. Even with such a database we, face the difficult task of trying to account for any perceived trends in population numbers because of the need for additional adequate data on causative variables. Peterson *et al.* (1984) reported on evidence at Isle Royale supporting a predicted cycle of 38 ± 13 years for moose-sized prey and hypothesized on the strong relationship between cycle periodicity and generation length. Wolff (1980) also suggested that heavy browsing by hares reduced the quality of moose feeding areas and may have predisposed moose to higher rates of wolf (*Canis lupus*) predation as moose condition declined.

Our purpose in this paper is three fold: (1) to present managers with a dataset consisting of 34 consecutive years (1955-1988) of information on moose population numbers, number of moose killed by hunters, and the number of days spent hunting for 4 regions of Saskatchewan; (2) to examine these data for regularity of fluctuations in population numbers over the 34 year period; and, (3) to assess the relationship between population fluctuations and hunter kill and hunter effort. To our knowledge, this dataset is the most complete continuous information on these variables for any jurisdiction in Canada. We recognize that even 34 years is a relatively small time period for a species with a life span exceeding 15 years. We therefore stress that this analysis is primarily exploratory.

STUDY AREA

To accommodate regional vegetation and habitat differences, the best provincial moose range within the mixedwood section of the commercial forest was subdivided into four distinct areas for this analysis (Figure 1). Trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) dominated the hardwood and mixedwood associations of the West and Hudson Bay blocks compared to the Central area where coniferous species were most abundant; the Cumberland block forms most of the Saskatchewan River Delta, a 3000 km^2 area characterized by a mix of lowlands, open meadows, expanses of willow flats, and forested levees in association with a network of streams and river channels. All areas support wolf and black bear

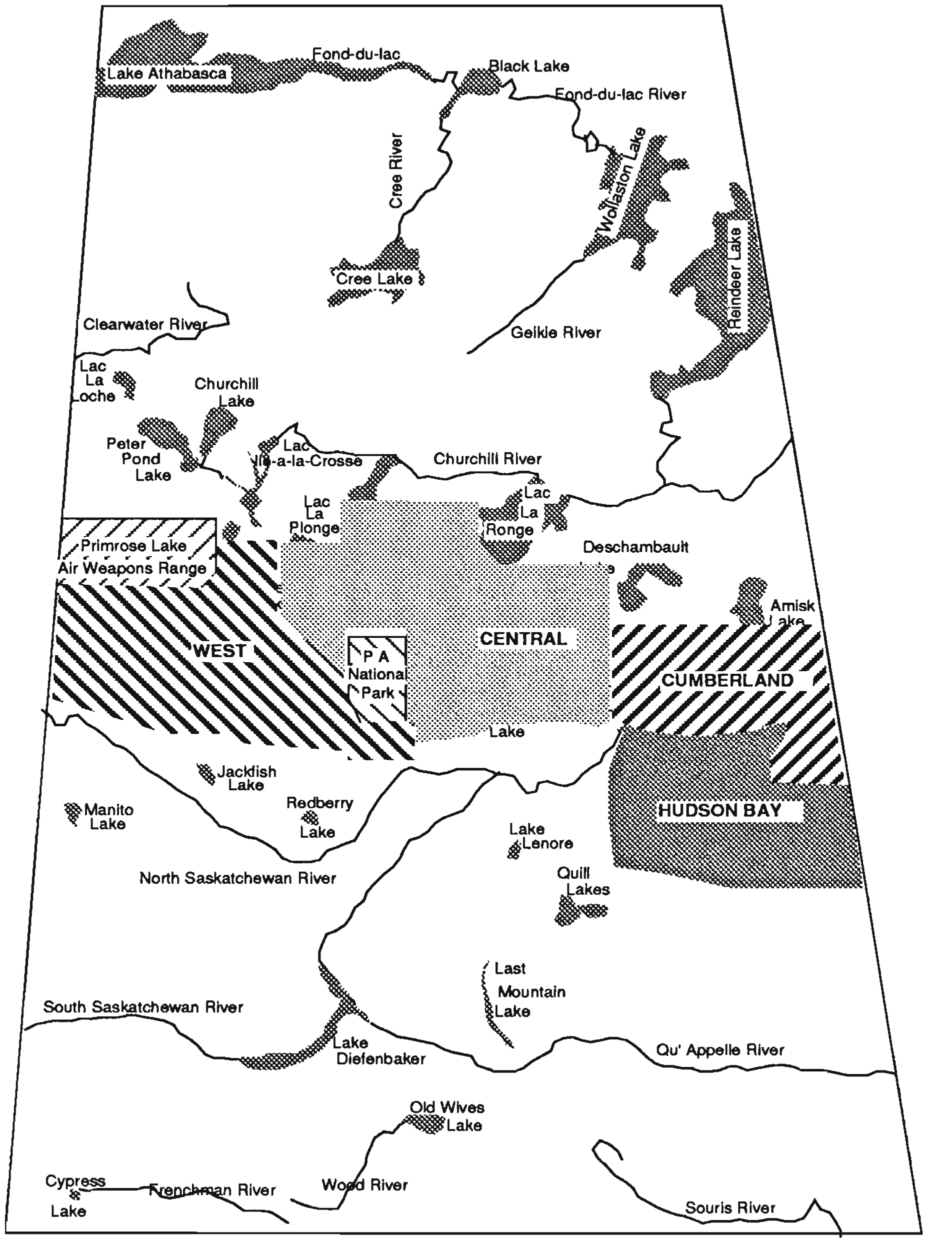

Figure 1. Location of four study areas in the commercial forest zone of Saskatchewan.

(*Ursus americanus*) populations; both prey on moose throughout their Saskatchewan range.

METHODS

Moose population trends were obtained from transect aerial surveys flown annually in January-February from 1955-1988 in small fixed-winged aircraft. Two observers, seated on opposite sides of the aircraft recorded all moose sighted within 195 m on each side of the aircraft which was flown at 120 m altitude and 150-160 km/hr. Flight patterns were oriented from systematic transect lines drawn on 1:250,000 scale topographic maps.

A number of different survey blocks have existed within each of the 4 areas over the 34 year history of aerial moose surveys. Specific information respecting the actual day and month, aircraft used, ambient weather conditions and snow cover do not accompany most of the historical data record. The impact of these variables on visibility bias has been well documented; therefore, we do not wish to suggest these data are collected according to any rigid standard. Total kill and hunter recreation data were obtained from records summarizing information obtained from annual hunter questionnaires for the period 1959-1987 (SPRC 1959-1987).

The number and size of the survey blocks and therefore the actual areas surveyed varied from year to year for each region; as a result the moose population estimates were divided by the size of the census areas to produce population density estimates. All data used in this study were tested for normality (normality plots and Wilks-Shapiro test) and, since the data constitute a time series, also for autocorrelation.

Population density values were plotted and visually examined for trends over the time period 1955-88. Trend lines were constructed for moose population densities for each study region. Semi-averages (the average value for each half of the time series) were calculated for the periods 1955-71 and 1972-88 and assigned to the middle year of the half. Population density fluctuations around the trend line for each study region were noted. Irregular fluctuations were reduced (or regular fluctuations highlighted) by the use of moving averages or running means for both the 5- and 9- year periods. The initial selection of the 5- year averages was arbitrary. The subsequent selection of 9- year averages was based on the examination of the plots of the 5-year averages. Plots were visually interpreted for possible cycling around the trend lines. Analyses of variance were conducted to assess differences in moose population densities, hunter effort, hunter kill and 5- 9- year moving averages among study regions. When significant differences were detected for a variable, the Student-Neuman-Kuels 'a posteriori' technique was used to determine which of the 4 study regions contributed to the overall difference.

Regression lines using the least-squares method with 95% confidence bands for the true means were drawn for the moose population densities for each study region. The significance of each regression slope from an hypothesized slope of 0 was assessed using a Student's t test. Polynomial regression equations were also calculated to assess their fit to the moose density data.

The relationship of variations in the number of moose killed by hunters (hunter kill) to variations in moose densities and numbers was assessed. Pearson's product-moment correlation coefficients and Spearman's rank correlation coefficients were calculated to assess the relationship between (1) moose population density and hunter kill for the same year as well as the previous year (time lag effect); (2) moose population density and hunter effort (defined as the number of hunter kills divided by the number of hunter days) for the same year and also for the previous year; and, (3) moose population estimates and hunter kill for the same year and for the previous year.

RESULTS

The complete dataset for all variables for the 34 year time period is given in Appendix 1. Normality tests on all variables showed no significant deviations from a normal distribution. Serial autocorrelation was noted for moose population density values for the Cumberland, Central, and West study regions but for no other variables.

Figure 2 shows plots of moose density estimates and semi-average trend lines for the 4 study regions. The results suggest increasing moose population densities for the Hudson Bay region and possibly the west region and no discernible trend for the re-

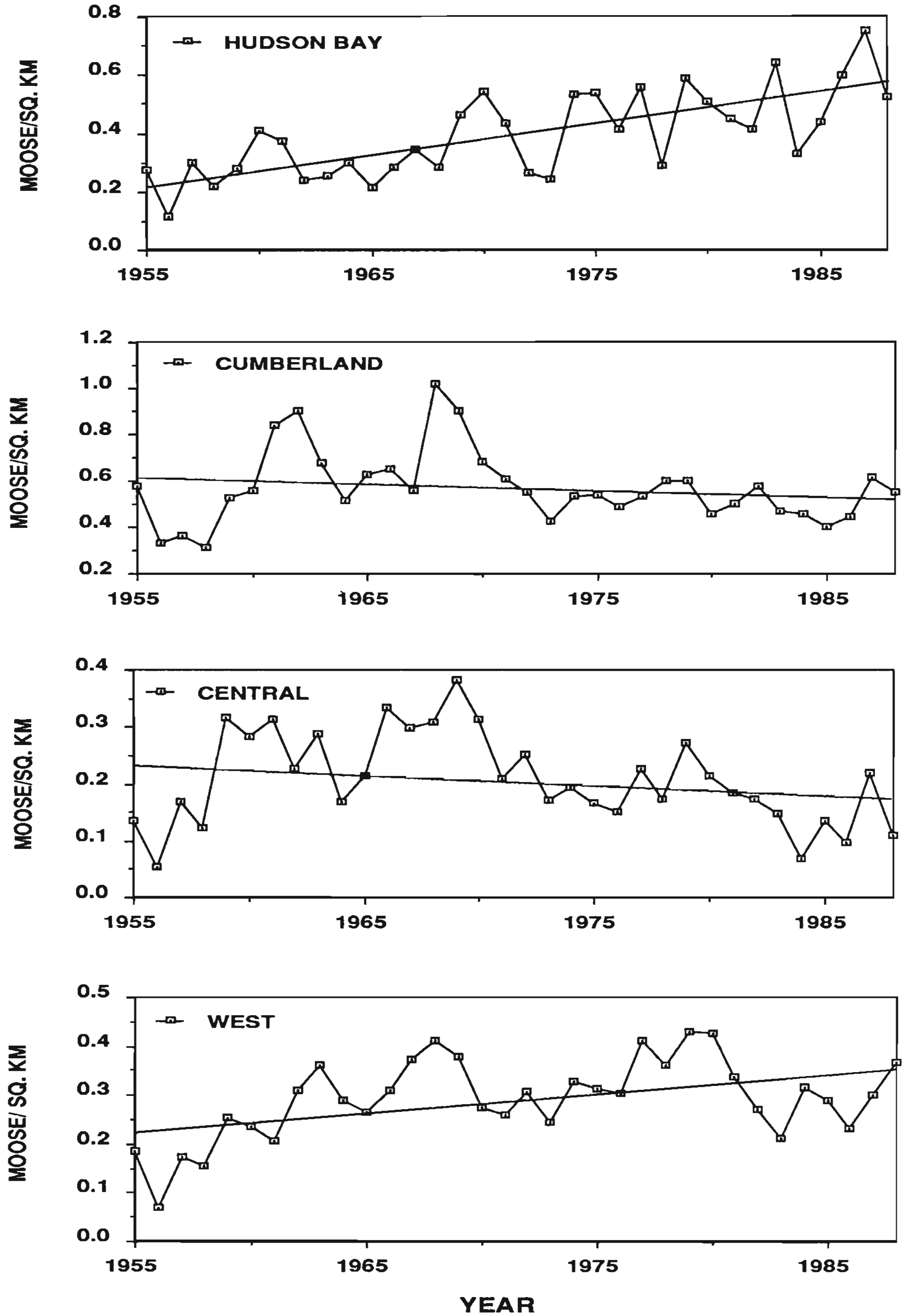

Figure 2. Population transect density estimates and semi-averages of population trend for the period 1955 - 1988.

maining 2 regions. Analyses of variance indicated that: (1) moose population densities were significantly different among the 4 study regions; (2) hunter effort for Hudson Bay was significantly different from the other 3 study regions which were similar; and, (3) hunter kills of moose were similar between Hudson bay and Cumberland and between Central and West, although the pairs were significantly different from each other.

The results of regression analysis showed a significant increase in moose population densities for the Hudson Bay and West study regions over the period 1955-1988, but not for the remaining 2 regions. There were no significant regressions of hunter effort with moose density for any study region.

Five and 9- year moving averages were calculated for the moose density values for each region and curves of population trends were fitted by eye (Figure 3). Analysis of variance results showed that the study regions were different from one another in the slope of the trend lines indicated by the 5- year moving averages. However, the plot of 5- year moving averages suggests a common wavelength of approximately 9-11 years for each study area with cycles commencing in 1960-61, 1971-72 and 1981-82. Analysis of variance for the 9-year moving averages indicates that Hudson Bay was similar to West and West similar to Central with Cumberland different from all other regions. The plot of 9- year averages also showed a cyclicity of 9-11 years with breaks in cycles occurring at relatively the same time periods. Of particular importance appear to be the time periods of the early 1960's and the early 1970's for all 4 study regions, the late 1970's for the Hudson Bay and West regions, and the early 1980's for Cumberland and Central.

Hudson Bay showed significant positive correlation between moose density and hunter effort, and Cumberland a significant negative correlation over the 34 year time period. Both Cumberland and Central moose densities were significantly negatively correlated with their hunter effort from the previous year. When direct moose population estimates, rather than densities, were correlated with hunter kill, rather than hunter effort, both Cumberland and Central showed a significant correlation between moose numbers and hunter kill of the previous year.

DISCUSSION

Regular oscillations in animal abundance have been demonstrated for numerous invertebrate and small vertebrate populations. Most students of these phenomena have attempted to isolate singular causative factors like food, stress, genetics, or predation as the driving force behind this population behaviour (Krebs 1970, Christian and Davis 1970). However, few researchers have reported on cyclicity in longer-lived mammals. This does not suggest that large mammals do not cycle, only that adequate datasets do not exist to test these hypothesis. Peterson *et al.* (1984) evaluated moose population data from an unhunted population on Isle Royale from the position that large, long-lived mammals would fluctuate at longer intervals than small species. They presented evidence on the effect of body size on the periodicity of the cycle and population dynamics in general, and of the dominant role played by the rate of increase in the dynamics of cycling species. They concluded that time lags in strong regulatory feedback mechanisms tend to produce an overshooting of equilibria and over-compensation, sometimes resulting in continual population oscillations.

However, our data also suggests the existence of shorter regular cycling with a 9-11 year periodicity in 4 Saskatchewan moose populations We do not wish to suggest that we understand the reasons for the 'apparent' regularity of the observed cycles in these populations. This is a difficult task and beyond the scope of this presentation. Stewart (1985) evaluated population data in relation to various hunting strategies deployed by

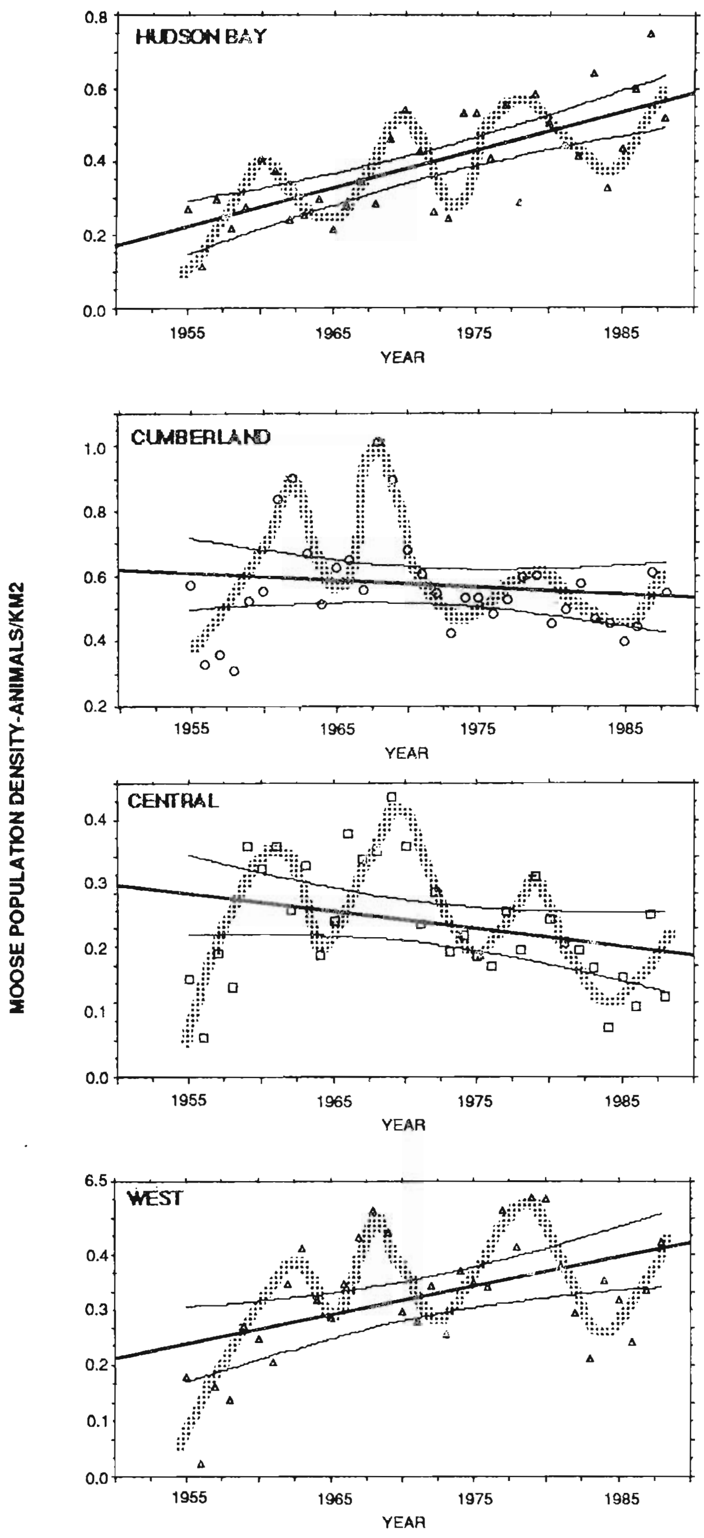

Figure 3. Regressions, 95% confidence bands of true means and curves of population density trends fitted by eye.

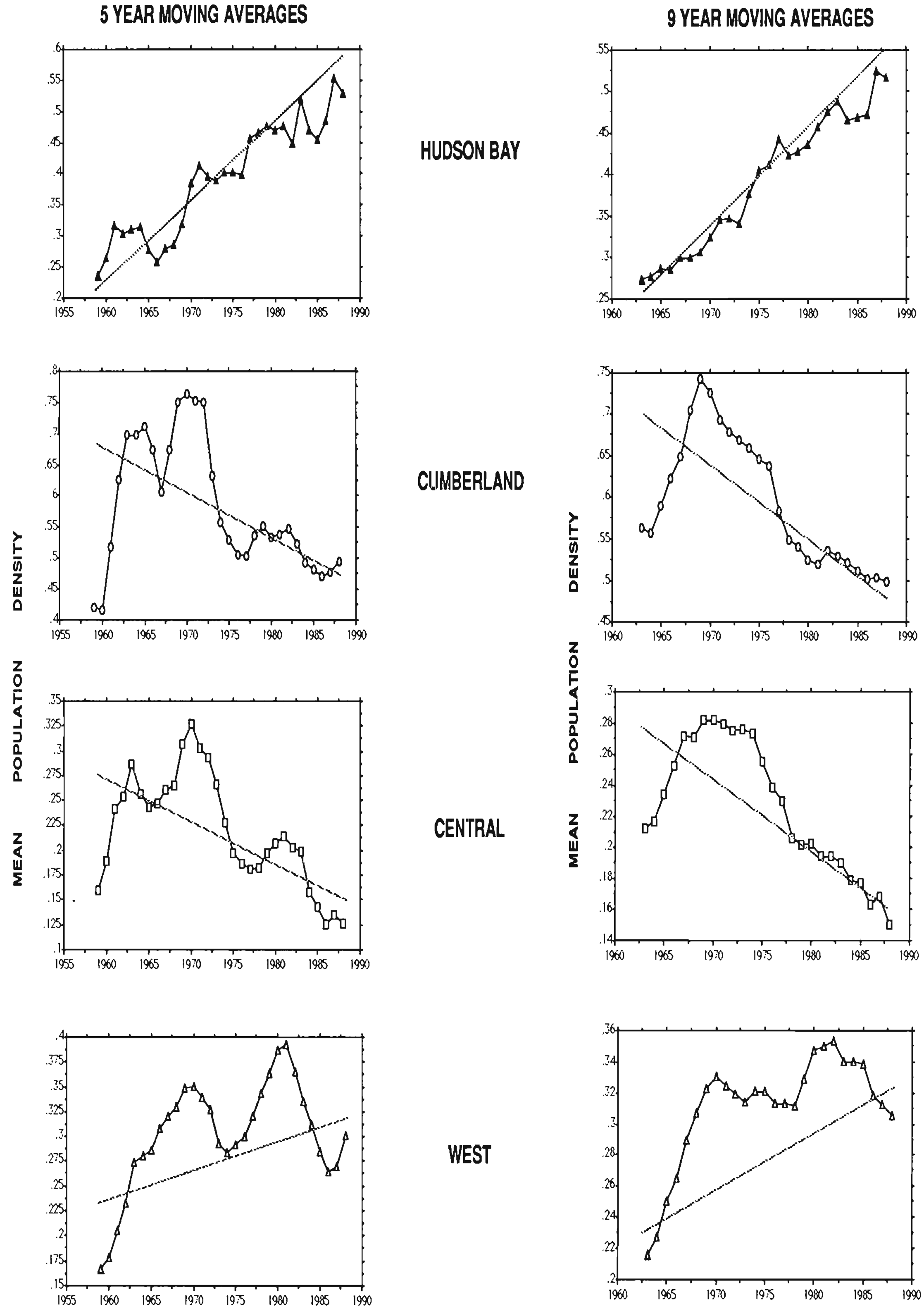

Figure 4. Five and 9 year moving averages of moose population densities for the 4 study regions.

moose managers in Saskatchewan in the period 1955-83. He was unable to demonstrate any positive long term correlation between hunter activity and population trends. He did suggest that the combination of high hunter pressure on a declining population had dramatic impacts on the structure of the harvests, with the moose kill profile dominated by adult animals. However, in other instances, high hunter pressure failed to prevent continued growth of an increasing population and conversely, low hunter pressure did not prevent further losses to a declining herd. In addition, the Saskatchewan moose population was considered sufficiently low in the late 1940's to warrant closure of all hunting seasons for 7 years (1946-52 inclusive). Is this further evidence of another wave in the reported cycle?

Moose populations in Saskatchewan are affected by a host of variables which may singly or in concert contribute to the reported oscillations; black bear and wolf predation, hunting pressure, tick (*Dermacentor albipictus*) infestations, and habitat change (logging and fire) are but a few of the agents which can effect changes in population productivity and mortality. The possibility of moose and snowshoe hare (*Lepus americana*) cyclic synchrony is also worth further investigation. Poor quantitative data exists in Saskatchewan regarding the temporal nature of hare population cycles. However, severe depredation of forest plantations were reported in 1970-71 and 1979-80, and hare populations are approaching high levels in 1988/89 and we are predicting a cyclic peak for 1990. Keith *et al.* (1984) reported cyclic peaks for 1961, 1970, and 1980 at Rochester, Alberta and commented on the wide geographic sweep and synchrony of the cylce in North America. These data fit well with our information which demonstrate moose populations highs at the start of each decade.

Substantially more effort is warranted in defining moose population cycles in other juridictions, identifying causative agents, constructing population models. An improved understanding of this phenomena should stimulate moose managers to adopt creative strategies to minimize the amplitude of the cycles.

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Appendix 1. Trend density, hunter pressure and harvest for 4 moose populations in Saskatchewan, 1955-88.

YEAR	DENSITY(/KM2)				HUNTERDAYS				HARVEST			
	H.B.*	C*	CL*	W*	H.B.	C	CL	W	H.B.	C	CL	W
1955	.271	.574	.134	.185	•	•	•	•	•	•	•	•
1956	.112	.331	.054	.067	•	•	•	•	•	•	•	•
1957	.298	.36	.168	.173	•	•	•	•	•	•	•	•
1958	.219	.311	.122	.154	•	•	•	•	•	•	•	•
1959	.277	.523	.315	.254	7553	10491	4714	2714	910	1264	568	327
1960	.409	.554	.284	.236	14992	9727	6583	2851	2503	1624	1099	476
1961	.374	.837	.314	.205	14810	11148	7318	4845	2204	1659	1089	721
1962	.239	.903	.228	.311	•	•	•	•	1213	1434	1130	721
1963	.252	.674	.289	.359	•	•	•	•	864	842	623	483
1964	.299	.514	.167	.288	•	•	•	•	953	1265	722	576
1965	.214	.626	.213	.265	•	•	•	•	863	1247	847	645
1966	.281	.653	.333	.311	9894	13392	10725	6803	970	1313	1051	667
1967	.345	.558	.298	.373	13896	14239	10064	7389	1418	1453	1027	754
1968	.283	1.018	.308	.411	13553	21096	12434	9038	1369	2131	1256	913
1969	.464	.899	.382	.379	14996	26275	13060	11227	1456	2551	1268	1090
1970	.54	.681	.314	.273	17281	23254	15505	9592	2708	3082	1774	1326
1971	.43	.606	.208	.26	15262	20992	19793	10931	2462	2902	2073	1504
1972	.261	.547	.251	.307	6407	13102	24885	12522	414	903	1304	1052
1973	.243	.425	.17	.243	4484	10237	8799	4388	534	978	558	375
1974	.532	.532	.193	.328	8045	6793	7451	5027	615	539	506	390
1975	.535	.536	.165	.313	12603	6840	8012	7651	725	465	560	495
1976	.411	.486	.151	.305	10197	7061	2032	6498	1097	707	202	570
1977	.556	.53	.226	.41	19376	11149	8742	9321	1421	1030	663	697
1978	.289	.598	.172	.36	16023	10697	8470	10491	1232	1109	527	786
1979	.584	.601	.273	.428	20977	13247	9631	13756	1325	819	588	952
1980	.505	.456	.214	.427	19874	10767	8148	12375	1808	1218	645	1214
1981	.448	.501	.184	.335	17142	10859	7540	11955	806	444	344	576
1982	.414	.578	.172	.27	17425	11458	7138	10303	954	646	284	622
1983	.643	.471	.149	.21	16748	9265	4852	6019	980	470	221	387
1984	.329	.458	.068	.315	17853	6296	3745	5297	1635	508	304	614
1985	.438	.401	.136	.288	20403	6918	4408	8206	1026	356	137	444
1986	.598	.444	.097	.232	26107	7528	4527	7930	1781	568	292	648
1987	.75	.612	.22	.302	•	•	•	•	•	•	•	•
1988	.522	.55	.11	.366	•	•	•	•	•	•	•	•

*H.B-Hudson Bay, C- Cumberland, CL-Central, W-West