

CAN HUMAN PREDATION OF MOOSE CAUSE POPULATION CYCLES?

Steven H. Ferguson and François Messier

Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK, S7N 5E2, Canada

ABSTRACT: The demography of a moose population in central Newfoundland was investigated using hunter statistics and cohort analysis to estimate moose density. The moose population occurs in a forested area of relatively high primary productivity for which trophic dynamics theory predicts regulation of herbivores by predation. No natural predators capable of density dependent regulation of moose live in Newfoundland. Therefore, we assessed the regulatory effects of human hunting on moose density. We used phase plots rather than time series to help describe nonlinear system dynamics. This approach characterized the behaviour of the human-moose system as a stable limit cycle with a period of about 11 years. Fluctuations in the prey population were tracked over time by fluctuations in the numbers of predators (number of hunters), predator searching time (hunter effort), and predator kills (harvest). The functional response of hunters reached an asymptote at densities greater than 1.4 moose·km⁻². Although the total response indicated a stable equilibrium due to density dependent hunting, we argue that cyclical behaviour in the numerical response leads to instability and population cycles. The regulatory effect was caused by delayed density dependence due to the time lag in the management response (number of licences) to changes in moose numbers. However, changes in food may have also had a delayed response and should be considered as a possible influence on synchronizing population cycles.

ALCES VOL. 32 (1996) pp.149-161

The North American moose (*Alces alces*) is a non-migrant species inhabiting mainly the boreal forest (Kelsall 1987). Moose populations living with predators generally exhibit densities below 0.5 animals·km⁻² (Messier 1994). In contrast, moose populations without major predators may exceed 2.0 animals·km⁻² (Cederlund and Sand 1991, Oosenbrug and Ferguson 1992). Food exploitation and predation are the two regulatory mechanisms proposed to explain moose population persistence (Boutin 1992, Van Ballenberghe and Ballard 1994, Messier 1995).

One hypothesis used to explain animal distribution and abundance in terrestrial environments is the HSS model (Hairston, Smith and Slobodkin 1960). According to this trophic dynamics model (see Oksanen *et al.* 1981, Fretwell 1987, Oksanen 1991), environments with relatively high primary productivity (i.e. three-level systems) are char-

acterized by plants and carnivores being resource-regulated (green world) while herbivores are regulated by predation. In environments with a primary productivity below a threshold (Power 1992), predation no longer regulates herbivores and herbivores may reduce plant biomass to low levels (brown world).

The island of Newfoundland supports both three- and two-level trophic environments and therefore, studies of plant-herbivore-carnivore interactions may help test some of the HSS model predictions (see Crête and Manseau 1996). The Northwest Gander-Gambo Moose Management Area (MMA 24&42) is situated in the forested central part of Newfoundland and occurs in a region characterized by relatively high primary productivity (Mercer and Manuel 1974). For this area, the HSS model predicts that predation will regulate prey population numbers. But wolves (*Canis lupus*) no longer exist on

the island of Newfoundland; black bear (*Ursus canadensis*) predation is not considered a mortality factor that regulates moose numbers (Ballard *et al.* 1991, Schwartz and Fanzmann 1991, Ballard 1992); and the recent arrival of coyotes (*Canis latrans*) is unlikely to have any regulatory impact on moose populations. In the absence of wolves, what is the form of regulation by humans (*Homo sapiens*) on moose numbers?

Many moose populations exhibit remarkable variations in abundance (Crête 1987, Gasaway *et al.* 1992). Some moose populations show regular cycles, such as in Alaska (Gasaway *et al.* 1983), on Isle Royale (1-cycle: 38 years; Peterson *et al.* 1984) and in Newfoundland (Moose Management Area 17, 4-cycles: 9.0 ± 1.3 (SE) years; Ferguson 1993), which have gone through 2- to 3-fold changes in density. Here, we report on a moose population with a large human hunting harvest (22% per annum) and bear predation on calves, that also shows cyclicity. The major mortality for moose in central Newfoundland is human predation through legal hunting. Cyclical dynamics may be driven by the kind of ecological conditions to which the species is exposed (Berryman 1995) or by the organism and its biological attributes (Bonner 1965, Calder 1984). Here, we empirically test whether human predation drives population cycles in this moose population.

STUDY AREA

Northwest Gander-Gambo MMA 24&42 (2,111 km²) is an area of central Newfoundland that has supported moose since the 1910s (Pimlott 1953). Besides humans, black bears have been the only natural predators of moose. Brown bears (*Ursus arctos*) do not live here, wolves were exterminated, and coyotes are a recent arrival to the island (Larivière and Crête 1993) and likely did not influence the population dynamics of moose in this area prior to the last 1991 estimate. The majority of hunters use

highway or fourwheel drive vehicles to reach their hunting areas whereas in less accessible areas, hunters rely more on aircraft, all terrain vehicles, boats and canoes (Crête 1987). Since 1972, Newfoundland has used a quota system whereby hunters are drawn for particular age/sex classes of moose and hunt in areas depending on priority (Mercer and Manuel 1974).

This study area lies within the Central Newfoundland ecoregion (Damman 1983) and is mostly covered by boreal forest. *Abies balsamea* predominates and stands of *Picea mariana*, and to a lesser extent *Betula papyrifera*, cover large areas. A dense moss carpet occurs in areas not disturbed by fire but this region experiences the highest forest fire frequency of the island. The continental climate in this area shows a large annual range in temperatures for the island with high summer temperatures and low winter temperatures. This area receives lower rainfall than other subregions as well as occasional dry spells. Growing season is 140-160 days. Precipitation and snowfall is average relative to most of the island with snow cover in winter being more reliable.

METHODS

Ecologists traditionally think in terms of time series as a way to represent population dynamics. Although conceptually straightforward, a time series plot (e.g. Fig. 1) is often of limited value for representing long-term dynamics and does not provide much insight into the dynamical structure of the system. As an alternative to a time series, mathematicians typically plot concurrent values of state variables on independent axes. The state-variable space generated by this process is called phase space, and the graph of state variables in a phase space is termed a phase plot. Plotting system dynamics in phase space, as opposed to a time series, has the distinct advantage of collapsing the system's dynamics along the time axis, thereby solv-

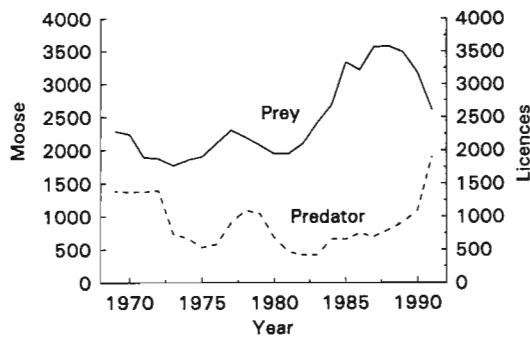


Fig. 1. Time series plot of predator (number of licences) and prey (moose numbers) from 1969 through 1991 in the Northwest Gander-Gambo Management Area, Newfoundland.

ing the logistic problem of plotting long-term behaviour. A phase space graphic facilitates the understanding of ecological systems in qualitative terms (Logan 1991). Phase plots are similar to numerical response plots but while ecologists expect numerical responses to be represented by a non-linear relationship (e.g. Fryxell 1991), phase plots portray system behaviour as an attractor of various shapes (Çambel 1993).

Plotting the relationship between predator and prey density helps to describe the behaviour of a system. In contrast, plotting the relationship between the functional response of predators and prey density helps to determine the mechanistic processes of the system. To understand the mechanistic process behind predator-prey relationships we plotted rates of change against prey density. One relationship we wanted to examine was the predators' success rate relative to prey density. Another relationship examined was the functional response of predators (killing rate) relative to prey density. This relationship took the form of a Type II functional response (Taylor 1984) as in many other systems (Real 1979, Messier 1994). We determined the functional response using the hyperbolic, Michaelis-Menten function which takes the form $y = ax/(b+x)$, where y is

the per capita killing rate and x is moose density (Messier 1994). Parameter a represents the asymptotic killing rate when predators are fully satiated, and b is the moose density at half the maximum killing rate. The last relationship examined was that of predation rate relative to prey density. The predation rate was calculated as the product of the numerical and functional responses and a third-order polynomial was used to fit the curve.

Cohort analysis requires time series data on age-specific kills and age-specific natural mortality rates and a large cumulative mortality (Pope 1972). We used Deriso *et al.*'s (1985) cohort analysis model (CAGEAN) to estimate moose density. Methods follow that of Ferguson (1993) with one difference; we did not follow Gulland's (1983) recommendation to average hunter effort. We decided that averaging unnecessarily smoothed the natural variability in the data. Although the estimated numbers of moose (Wilcoxon Mann-Whitney test: $Z = -2.13$, $P = 0.03$) and their variation ($F_{1,21} = 5.87$, $P < 0.001$) differed between the two approaches, the overall distribution of estimates did not differ significantly (Kolmogorov-Smirnov 2-sample test: $D = 0.348$, $KSa = 1.18$, $n = 23$, $P = 0.12$). All statistical tests were done using SAS (SAS Institute Inc., Cary, NC) statistical software for microcomputers.

RESULTS

From 1969 to 1991, predator and prey numbers in the Northwest Gander-Gambo Management Area markedly fluctuated over time (Fig. 1). Predator numbers varied 4- to 5-fold from 420 to 1896 licences (895 ± 382 (SD)) while prey numbers varied 2-fold from 1772 to 3577 moose (2461 ± 617 ; Table 1).

Phase plots of predator numbers (numerical response; Fig. 2), predator kills (Fig. 3) and predator effort (Fig. 4) against prey density all followed a closed-loop pattern in

Table 1. Moose population statistics for Northwest Gander-Gambo MMA, central Newfoundland.

Year	Estimated No. of Moose ¹	Per-Capita Rate of Increase	Hunter Effort (days)	No. of Licences (hunters)	No. of Moose Killed	Kill/Licence	Killing Rate ²	Predation Rate ³
1969	2289	-	7479	1384	518	0.37	6.9	22.6
1970	2239	-0.02	7751	1376	822	0.60	10.6	36.7
1971	1892	-0.17	7843	1379	529	0.38	6.7	28.0
1972	1872	-0.01	8089	1394	578	0.41	7.1	30.9
1973	1772	-0.05	4419	740	292	0.39	6.6	16.5
1974	1853	+0.04	3518	678	347	0.51	9.9	18.7
1975	1907	+0.03	2894	537	287	0.53	9.9	15.0
1976	2108	+0.10	2582	582	362	0.62	14.0	17.2
1977	2308	+0.09	4923	900	584	0.65	11.9	25.3
1978	2202	-0.05	6826	1100	654	0.59	9.6	29.7
1979	2076	-0.05	7184	1050	513	0.49	7.1	24.7
1980	1951	-0.06	4561	690	402	0.58	8.8	20.6
1981	1952	+0.00	3031	470	268	0.57	8.8	13.7
1982	2104	+0.07	2340	420	293	0.70	12.5	13.9
1983	2422	+0.14	2254	420	309	0.74	13.7	12.8
1984	2688	+0.10	3571	660	461	0.70	12.9	17.2
1985	3336	+0.22	3263	660	449	0.68	13.8	13.5
1986	3218	-0.04	3677	750	530	0.71	14.4	16.5
1987	3568	+0.10	5097	700	638	0.91	12.5	17.9
1988	3577	+0.00	6164	800	758	0.95	12.3	21.2
1989	3489	-0.02	6590	915	872	0.95	13.2	25.0
1990	3181	-0.09	6028	1090	891	0.82	14.8	28.0
1991	2610	-0.20	10293	1896	941	0.50	9.1	36.1
Mean	2461	+0.01	5234	895	535	0.62	10.8	21.8
SD	617	6.8	2231	382	209	0.17	2.7	7.2

¹ Estimated using cohort analysis and includes crippling loss and poaching.

² Killing rate = moose killed/(licence·100 days⁻¹).

³ Predation rate = total moose killed/total moose alive at the start of the hunting season (percent of population killed by hunters each year).

an anti-clockwise direction. The system's dynamics cycled in what mathematicians term a limit cycle. Anti-clockwise cyclic patterns over time can be indicative of delayed density dependence, sometimes termed delayed negative feedback (Hutchinson 1948).

Evidence for time lags causing this negative feedback came from partial correlation analysis of lagged hunter statistics. First, the effect of first-order correlation, PC1, between $R = \ln(N_{t+1}/N_t)$ and $\ln N_t$ was determined. Next, the relative contribution of sec-

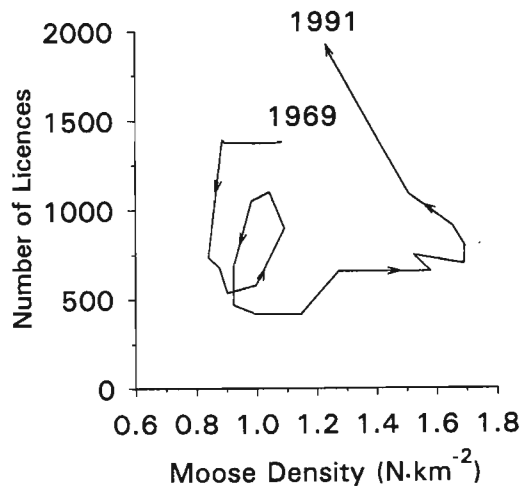


Fig. 2. Changes in the number of predators (human hunters) with prey density (moose) from 1969 through 1991 in the Northwest Gander-Gambo Management Area, Newfoundland.

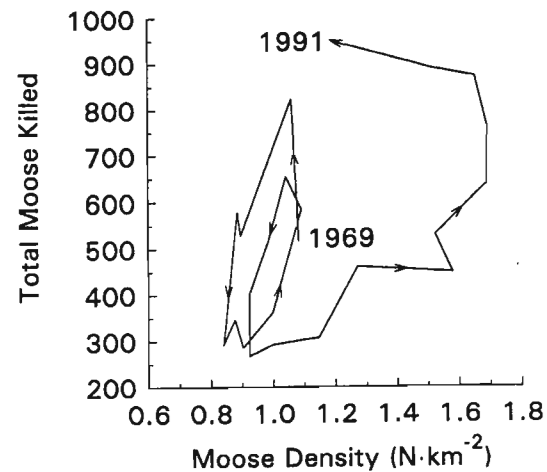


Fig. 4. Phase plot of predator kills (moose killed by hunters) with prey (moose) density from 1969 through 1991 in the Northwest Gander-Gambo Management Area, Newfoundland.

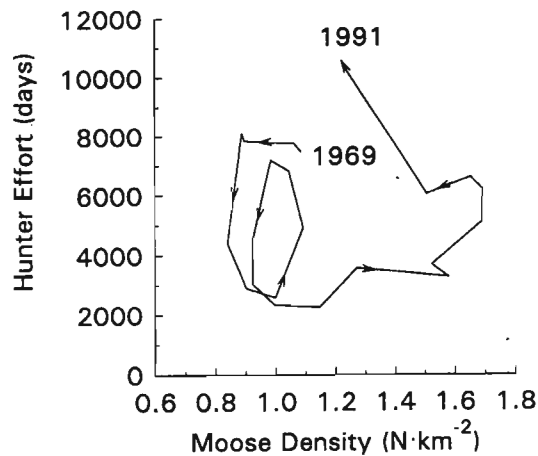


Fig. 3. Phase plot of predator effort (hunter days) with prey (moose) density from 1969 through 1991 in the Northwest Gander-Gambo Management Area, Newfoundland.

ond-order feedback to the observed dynamics was calculated as the partial correlation, PC2, between the observed per-capita rate of increase, R , and population density in the previous year,

In N_{t-1} , from which the effect of first-order correlation, PC1, had been removed (Table 2). Cyclical dynamics are dominated by second-order feedback ($PC2 > PC1$), while

those with more stable dynamics are dominated by first-order feedback ($PC2 < PC1$). For this predator-prey system, moose density, predator density, and predator effort were all dominated by second-order feedback implying delayed density dependence (Table 2).

Next, we looked at the relationship between rates of change for predation variables relative to density. Hunter success increased linearly with moose density ($r = 0.83$, $n = 22$, $P < 0.01$; Fig. 5). The Type II functional response of human predation was related to moose density using the Michaelis-Menten model ($r = 0.66$, $n = 22$, $P < 0.01$; Fig. 6). The killing rate increased at low moose densities and reached an asymptotic value of 15.5 moose killed/(hunter·100 days⁻¹) indicating some form of predator satiation. The moose density associated with half the maximum killing rate was 1.2 moose·km⁻².

Predation rate or total response was calculated as the percent of the moose population harvested by hunters (Fig. 7). This relationship indicates strong density dependent predation at moose densities of less than 1.4 moose·km⁻². For the central

Table 2. Properties of a cyclical moose population in central Newfoundland, 1971 through 1991.

Property	First-Order Rate Corr. ¹	Second-Order Partial Corr. ²	Coefficient Multiple Determination ³	Significance ⁴	
				N_t	N_{t-1}
Total Moose	0.277	0.443	0.548	0.12	0.03
Hunters (licences)	0.293	0.520	0.534	0.55	0.04
Hunter Effort (days)	0.327	0.539	0.547	0.67	0.04
Total Kill	0.469	0.399	0.475	0.23	0.72

¹ Correlation between the per-capita rate of change, $R = \ln(N_{t+1}/N_t)$, and the log initial population density, $\ln N_t$.

² Correlation between R and $\ln N_{t-1}$ with the effect of first-order correlation removed.

³ Coefficient of multiple determination for the model $R = a + b \ln N_t + c \ln N_{t-1}$.

⁴ Significance of correlation coefficient for N_t and N_{t-1} .

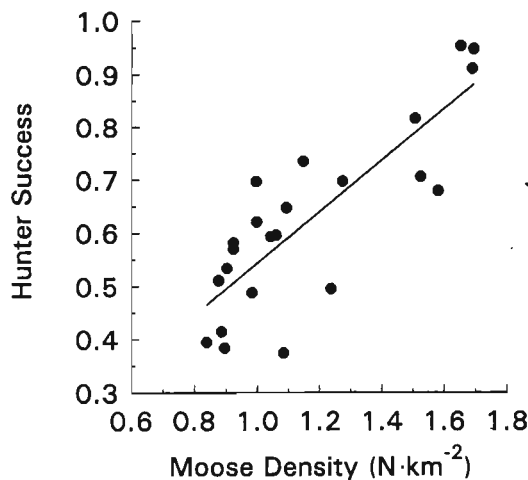


Fig. 5. Linear relationship of hunter success (moose kills per licensee) with moose density from 1969 through 1991 in the Northwest Gander-Gambo Management Area, Newfoundland.

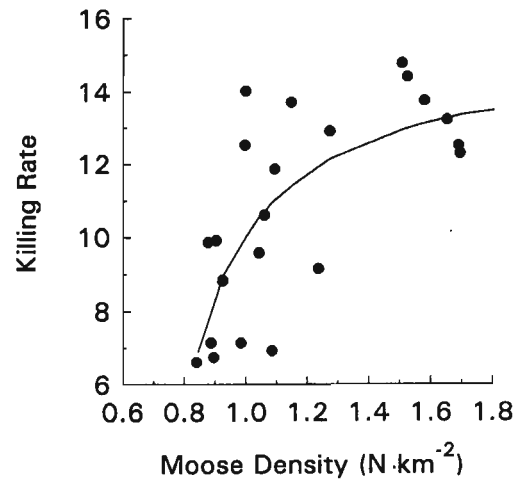


Fig. 6. Functional response of predators (moose killed/(hunter·100 days⁻¹) against moose density from 1969 through 1991 in the Northwest Gander-Gambo Management Area, Newfoundland.

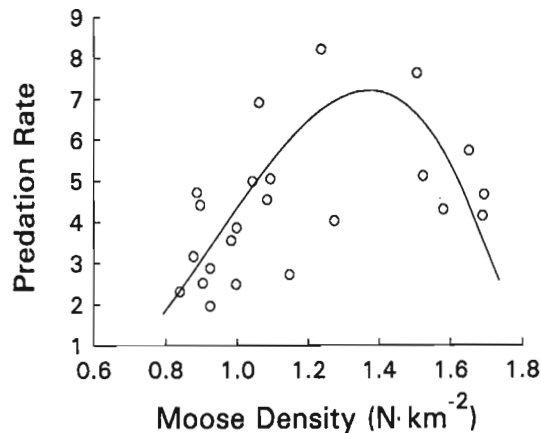


Fig. 7. Relationship between predation rate (percent harvest) and moose density from 1969 through 1991 in the Northwest Gander-Gambo Management Area, Newfoundland.

forested areas of Newfoundland, K_p , mortality due to human predation increased as density of moose increased through a density-dependent functional response. Time lags created in the numerical response resulted in population cycles. The density of prey is not fixed at these equilibria but instead are continually perturbed by changes in the environment. Moose densities greater than $1.4 \text{ moose}\cdot\text{km}^2$ experienced inversely density dependent human predation. The relative positions of the recruitment and total response curves result in two stable states K_p and K_c , with the low density state regulated by predation whereas the high density state occurred when the prey escaped predator regulation (Fig. 8).

DISCUSSION

These results indicate that human predation of moose is strongly density dependent within the lower range of moose density ($<1.5 \text{ moose}\cdot\text{km}^2$). This moose population shows dynamics that are strongly affected by second-order feedback processes (Turchin 1990), or what is traditionally called delayed density dependence (Morris 1959). Stable limit cycle behaviour is a result of non-linearity, which in predator-prey systems

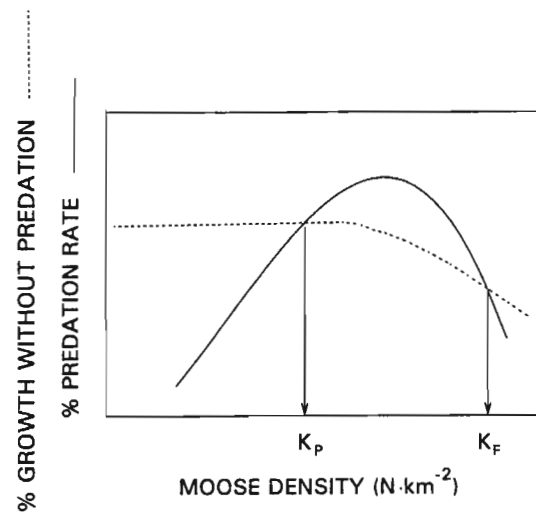


Fig. 8. A model for moose populations with strong density dependent human predation. Human predation (—) is density dependent at low moose densities and inversely density dependent at high moose densities. The growth rate of moose without human predation (---) declines at high density due to density dependent food limitation. K_p is a stable equilibrium around which cycles in the numerical response causes the moose population to cycle over time. K_F is an unstable equilibrium caused by the interaction between predation and food limitation.

implies that the effects of predation is non-proportional (Berryman 1996). Dynamics that cycle without damping, but are still bounded, are intriguing, but appear common in natural predator-prey systems (Norrdahl 1995).

What drives cycles?

Our main interest was in determining the major factor driving the cyclical behaviour of this moose population. External forces like climate or sunspot cycles are unlikely to drive the system although external forces are probably involved in the synchronization of cycles over large geographic regions (Moran 1953, Royama 1992). The next approach was to examine factors involved in circular causality, or negative feedback (Sinclair and Pech 1996).

Population cycles can be caused by time lags in any negative feedback process (May 1973, 1981, Berryman 1989). Therefore one plausible mechanism involves interactions with the food of moose. Time lags can be created if the quality of new foliage is affected by browsing in the previous year (delayed induced defence hypothesis, Batzli 1983, Seldal *et al.* 1994), or if high moose densities and/or food shortages in one year can affect the survival and fecundity of the next generation via physiological mechanisms (maternal effect hypothesis, McCullough 1979, Sauer and Boyce 1979, Peterson *et al.* 1984, Fryxell *et al.* 1991, Rossiter 1994).

There is evidence from other species that heavy browsing can cause marked changes in the quality of new foliage in the following years (Caughley 1976, McCullough 1979, Cooper and Owen-Smith 1985, Palo 1985, Lavsund 1987, Robbins *et al.* 1987, Thompson 1988). These changes can have a negative impact on the fitness of moose (Sæther 1987). There is also evidence that maternal experiences of red deer (*Cervus elaphus*) in one year can affect the fitness of offspring in succeeding generations (Clutton-Brock *et al.* 1982, Albon *et al.* 1987). Models incorporating food quality and maternal effects can generate cycles (Berryman 1996). However, to test the food hypothesis requires quantitative data on the effects of browsing on changes in foliage properties and the effects of food availability and quality on browsing rates during a population cycle (e.g., Krebs *et al.* 1986a, 1986b, 1992). Although we have no evidence, changes in food may have had a delayed response and should be considered as a possible influence on population cycles. Perhaps food changes synchronize the periodicity whereas predation determines the amplitude of moose population cycles.

Effects of human predation

This study of the cyclic behaviour of a

moose population has led us to conclude that human predators can cause cyclic dynamics. Humans invariably kill a high proportion of moose during the decline phase (Table 1) and relax their effects during the increase phase, a necessary property of predator-prey cycles. The effectiveness of human predators at controlling the numerical dynamics of their prey (moose) is further attested to by several examples of intense food limitation experienced by moose in areas of Newfoundland where inaccessibility limits the effectiveness of hunters (Ferguson *et al.* 1989). The present data on moose and human hunters over a 23-year period suggests that much of the annual variation in observed per-capita rates of change of this population can be explained by conventional predator-prey interactions.

We conclude that the 8-11 year cycles in moose numbers are probably caused by delayed negative feedback between human hunters and moose abundance. Examples of how delayed management responses can result in time lag effects have been reported for walrus (*Odobenus rosmarus*; Fay *et al.* 1989), white-tailed deer (*Odocoileus virginianus*; Fryxell *et al.* 1991) and in fisheries (McGarvey 1993). The cyclic dynamics can be exacerbated, however, by environmental disturbances and socio-political changes. Political events can result in sudden changes in numbers of hunters and include relatively unpredictable events such as the number of traffic related human deaths caused by moose collisions (Oosenbrug *et al.* 1991) or increased poaching. Environmental disturbances are more likely in the southern portion of the island, where little forest exists and the potential for particularly large die-offs of the moose population can occur (e.g. severe winter conditions such as icing) causing a temporary decoupling of the predator-prey interaction.

Many moose populations are regulated with relatively little variation at densities far below the food carrying capacity (Crête 1987,

Van Ballenberghe 1987, Gasaway *et al.* 1992, Messier 1995). Empirical evidence suggests that human predators are involved in the cyclical second-order dynamics, whereas wolves are involved in the more stable first-order dynamics (Messier 1994, 1995). We suspect that human searching efficiency is somehow compromised in regions where moose populations reach the limits set by their food supplies, perhaps because of lack of natural predators or area inaccessibility to hunters (Mercer and Manuel 1974). Management efforts to control destructive moose over-browsing are aided by human hunters, who are remarkably efficient at searching out and killing moose. Managers can capitalize on the knowledge that hunters, if largely unimpeded in their movements, can exercise density dependent effects on moose numbers.

New model

The maximum predation rate by humans hunting in this area occurred at densities of 1.4 moose·km⁻². This figure coincides with the carrying capacity calculated by Ferguson (1992) of 1.3 moose·km⁻² based on percent forest cover, indices of moose productivity, and evidence summarized by Crête (1989). We would therefore expect maternal effects as a result of food limitation to occur at moose densities greater than about 1.4 moose·km⁻² (Fig. 8). Although, the model presented in Figure 8 predicts that the lower equilibrium of moose density maintained by human predation is stable, we suggest that the cyclical behaviour observed in the numerical response promotes the cycles in moose density over time. The population cycles may be caused by time lags in changes in predator density, possibly due to reactive rather than proactive management decisions to adjust the number of licences issued. As observed for moose and caribou (*Rangifer tarandus*), a negative-sloped functional response at high prey densities results in a

depensatory predation curve (Dale *et al.* 1994, Messier 1995). If moose numbers cycle, then at high densities a depensatory population response can occur with resource exploitation dominating population regulation (Fig. 8; see also Messier 1991).

The moose population in our study area experienced regulation by human predation which maintained moose density within large bounds (1.17 ± 0.29, mean ± SD, range 0.84 to 1.69). Moose densities can be maintained by human predation for the same reasons that wolf predation is so effective in reducing moose population growth at low densities (Messier 1994). Moose are non-gregarious, well dispersed, show limited movement, small home ranges and are spatially predictable. After three decades of searching for the causes of animal population cycles in genetic feedback mechanisms, maternal effects, induced plant defences and disease, ecologists seem to be returning to the old ideas of predator-prey cycles in snowshoe hares (Trostel *et al.* 1987), microtine rodents (Hanski *et al.* 1991), insects (Berryman 1996) and curiously, moose in some areas.

ACKNOWLEDGEMENTS

We benefited from the constructive comments and criticisms of M. Crête, J.M. Fryxell, and J. Virgl. Financial support was provided to SF by a Graduate Scholarship from the University of Saskatchewan, and a NSERC operating grant to FM. Finally, thanks are extended to the many individual hunters who responded to survey questionnaires and the Newfoundland Wildlife Division for collection of the data.

REFERENCES

- ALBON, S. D., T. H. CLUTTON-BROCK, and F. E. GUINNESS. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. *J. Anim. Ecol.* 56:69-81.

- BALLARD, W. B. 1992. Bear predation on moose: a review of recent North American studies and their management implications. *Alces Suppl.* 1:162-176.
- _____, J. S. WHITMAN, and D. J. REED. 1991. Population dynamics of moose in south-central Alaska. *Wildl. Mono. No.* 114.
- BATZLI, G. O. 1983. Response of arctic rodent populations to nutritional factors. *Oikos* 40:396-406.
- BERRYMAN, A. A. 1989. The conceptual foundations of ecological dynamics. *Bull. Ecol. Soc. Am.* 70:234-240.
- _____. 1995. Population cycles: a critique of the maternal and allometric hypotheses. *J. Anim. Ecol.* 64:290-293.
- _____. 1996. What causes population cycles of forest Lepidoptera? *TREE* 11:28-32.
- BONNER, J. T. 1965. Size and cycle. Princeton Univ. Press, Princeton, N.J., 71 pp.
- BOUTIN, S. 1992. Predation and moose population dynamics: a critique. *J. Wildl. Manage.* 56:116-127.
- ÇAMBEL, A. B. 1993. Applied chaos theory: a paradigm for complexity. Academic Press, Boston.
- CALDER, W. A. III. 1984. Size, function, and life history. Harvard Univ. Press, Harvard.
- CAUGHLEY, G. 1976. Wildlife management and the dynamics of ungulate populations. Pages 183-246. *in* T. H. Coaker, ed. *Applied biology*. Vol. 1. Academic Press, London.
- CEDERLUND, G., and H. K. G. SAND. 1991. Population dynamics and yield of a moose population without predators. *Alces* 27:31-40.
- CLUTTON-BROCK, T. H., F. E. GUINNESS, and S. D. ALBON. 1982. Red deer: behavior and ecology of two sexes. Univ. Chicago Press, Chicago.
- COOPER, S. M., and N. OWEN-SMITH. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. *Oecologia* 67:142-146.
- CRÊTE, M. 1987. The impact of sport hunting on North American moose. *Swedish Wildl. Res. Suppl.* 1:553-563.
- _____. 1989. Approximation of K carrying capacity for moose in eastern Quebec. *Can. J. Zool.* 67:373-380.
- _____. and M. MANSEAU. 1996. Natural regulation of cervidae along a 1000 km latitudinal gradient: change in trophic dominance. *Evol. Ecol.* 10: 51-62.
- DALE, B. W., ADAMS, L. G., and R. T. BOWYER. 1994. Functional response of wolves preying on barren ground caribou in a multiple-prey ecosystem. *J. Anim. Ecology* 63: 644-652.
- DAMMAN, A. W. H. 1983. An ecological subdivision of the island of Newfoundland. Pages 163-206. *in* *Biogeography and ecology of the Island of Newfoundland*. Ed. G. R. South. W. Junk Publishers, Hague.
- DERISO, R. B., T. J. QUINN II, and P. R. NEAL. 1985. Catch-age analysis with auxiliary information. *Can. J. Fish. Aquat. Sci.* 42:815-824.
- FAY, F. H., B. P. KELLY, and J. L. SEASE. 1989. Managing the exploitation of Pacific walruses: a tragedy of delayed response and poor communication. *Marine Mammal Science* 5:1-16.
- FERGUSON, S. H. 1992. Newfoundland moose model I: harvest management based on relationship between productivity and vegetation. Unpubl. Int. Rept. Nfld. and Labr. Wildl. Divi. 36 pp.
- _____. 1993. Use of cohort analysis to estimate abundance, recruitment and survivorship for Newfoundland moose. *Alces* 29:99-113.
- _____, W. E. MERCER, and S. M. OOSENBURUG. 1989. The relationship between hunter accessibility and moose condition in Newfoundland. *Alces* 25:36-47.

- FRETWELL, S. D. 1987. Food chain dynamics: the central theory of ecology. *Oikos* 50:291-301.
- FRYXELL, J. M. 1991. Forage quality and aggregation by large herbivores. *Am. Nat.* 138:478-498.
- _____, D. J. T. HUSSELL, A. B. LAMBERT, and P. C. SMITH. 1991. Time lags in population fluctuations in white-tailed deer. *J. Wildl. Manage.* 55:377-385.
- 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.* 84:1-50.
- _____, R. D. BOERTJE, D. V. GRANGAARD, D. G. KELLEYHOUSE, R. O. STEPHENSON, and D. G. LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildl. Monographs*. 120:1-59.
- GULLAND, J. A. 1983. Fish stock assessment: a manual of basic methods. Wiley-Interscience Publ. John Wiley & Sons, New York. 223 pp.
- HAIRSTON, N. G., F. E. SMITH, and L. B. SLOBODKIN. 1960. Community structure, population control, and competition. *Am. Nat.* 94:421-425.
- HANSKI, I., L. HANSSON, and H. HENTTONEN. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* 60:353-367.
- HUTCHINSON, E. 1948. Circular causal systems in ecology. *Ann. NY Acad. Sci.* 50:221-246.
- KELSALL, J. P. 1987. The distribution and status of moose (*Alces alces*) in North America. *Swedish Wildl. Res. Suppl.* 1:1-10.
- KREBS, C. J., S. BOUTIN, and B. S. GILBERT. 1986a. A natural feeding experiment on a declining snowshoe hare population. *Oecologia* 70:194-197.
- _____, B. S. GILBERT, S. BOUTIN, A. R. E. SINCLAIR, and J. N. M. SMITH. 1986b. Population biology of snowshoe hares. I. Demography of food-supplemented populations in southern Yukon, 1976-1984. *J. Anim. Ecol.* 55:963-982.
- _____, R. BOONSTRA, S. BOUTIN, M. DALE, S. HANNON, K. MARTIN, A. R. E. SINCLAIR, J. N. M. SMITH, and R. TURKINGTON. 1992. What drives the snowshoe hare cycle in Canada's Yukon? Pages 886-896 in *Wildlife 2001: Populations*, D. M. McCullough, and R. H. Barret (eds.). Elsevier, London.
- LARIVIÈRE, S., and M. CRÊTE. 1993. The size of eastern coyotes (*Canis latrans*): a comment. *J. Mammal.* 74:1072-1074.
- LAVSUND, S. 1987. Moose relationships to forestry in Finland, Norway and Sweden. *Swedish Wildl. Res. Suppl.* 1:229-244.
- LOGAN, J. A. 1991. Chaos: much ado about something. Pages 1-22 in *Chaos and insect ecology*. Eds. J. A. Logan and F. P. Hain. Virginia Experimental Station Info. Ser. 91-3. Blacksburg: Virginia Polytechnic Institute & State Univ.
- MAY, R. M. 1973. Complexity and stability in model ecosystems. Princeton Univ. Press, Princeton, N.J. 235 pp.
- _____. 1981. Models for single populations. Pages 5-77 in *Theoretical Ecology Principles and Applications*, 2nd ed. R. M. May (ed.). Blackwell, Oxford.
- McCULLOUGH, D. R. 1979. The George Reserve deer herd: population ecology of a k-selected species. Univ. Michigan Press, Ann Arbor, 271 pp.
- McGARVEY, R., F.M. SERCHUK, and I.A. McLAREN. 1993. Spatial and parentage analysis of stock-recruitment in the Georges Bank sea scallop (*Placopecten magellanicus*) population. *Can. J. Fish.*

- Aquatic Sci. 50:564-574.
- MERCER, W. E. and F. MANUEL. 1974. Some aspects of moose management in Newfoundland. *Naturaliste can.* 101:657-671.
- MESSIER, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *J. Anim. Ecol.* 60:377-393.
- . 1994. Ungulate population models with predation: a case study with the North American moose. *Ecology* 75:478-488.
- . 1995. Trophic interactions in two northern wolf-ungulate systems. *Wildl. Res.* 22:131-146.
- MORAN, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Australian J. of Zool.* 1:291-298.
- MORRIS, R.F. 1959. Single factor analysis in population dynamics. *Ecology* 40:580-588.
- NORRDAHL, K. 1995. Population cycles in northern small mammals. *Biol. Rev.* 70:621-637.
- OKSANEN, T. 1991. Trophic levels and trophic dynamics: a consensus emerging? *TREE* 6:58-60.
- OKSANEN, L. S. D. FRETWELL, J. ARRUDA, and P. NIEMELA. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118:240-261.
- OSENBRUG, S.M. and S.H. FERGUSON. 1992. Moose mark-recapture survey in Newfoundland. *Alces* 28:21-30.
- , E. W. MERCER, and S. H. FERGUSON. 1991. Moose-vehicle collisions in Newfoundland: management considerations for the 1990's. *Alces* 27:220-225.
- PALO, R. T. 1985. Chemical defense in birch: inhibition of digestibility in ruminants by phenolic extracts. *Oecologia* 68:10-14.
- PETERSON, R. O., R. E. PAGE, and K. M. DODGE. 1984. Wolves, moose, and the allometry of population cycles. *Science* 224:1350-1352.
- PIMLOTT, D. H. 1953. Newfoundland moose. *Trans. 18th North Amer. Wildl. Conf.* 2 pp.
- POPE, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. *Bull. I-CNAF*, No. 9:65-74.
- POWER, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology* 73:733-746.
- REAL, L. A. 1979. Ecological determinants of functional response. *Ecology* 60:481-485.
- ROBBINS, C. T., T. A. HANLEY, A. E. HAGERMAN, O. HJELJORD, D. L. BAKER, C. C. SCHWARTZ, and W. W. MAUTZ. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* 68:98-107.
- ROSSITER, M. 1994. Maternal effects hypothesis of herbivore outbreak. *BioScience* 44:752-763.
- ROYAMA, T. 1992. Analytical population dynamics. Chapman & Hall.
- SÆTHER, B.-E. 1987. Patterns and processes in the population dynamics of the Scandinavian moose (*Alces alces*): some suggestions. *Proc. Int. Moose Symp.* 2:525-537.
- SAUER, J. R., and M. S. BOYCE. 1979. Time series analysis of the National Elk Refuge census. Pages 9-12 in M. S. Boyce and L. D. Hayden-Wing, eds. *North American elk: ecology, behavior and management*. Univ. Wyoming Press, Laramie.
- SCHWARTZ, C. C., and A. W. FRANZMANN. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. *Wildl. Monographs*. 113:1-58.

- Wildl. Monographs. 113:1-58.
- SELDAL, T., K.-J. ANDERSEN, and G. HOGSTEDT. 1994. Grazing-induced proteinase inhibitors: a possible cause for lemming population cycles. *Oikos* 70:3-11.
- SINCLAIR, A.R.E. and R.P. PECH. 1996. Density dependence, stochasticity, compensation and predator regulation. *Oikos* 75: 164-173.
- TAYLOR, R. J. 1984. Predation. Chapman and Hall, New York.
- THOMPSON, I. D. 1988. Moose damage to pre-commercially thinned balsam fir stands in Newfoundland. *Alces* 24:56-61.
- TROSTEL, K., A. R. E. SINCLAIR, C. J. WALTERS, and C. J. KREBS. 1987. Can predation cause the 10-year hare cycle? *Oecologia* 74:185-192.
- TURCHIN, P. 1990. Rarity of density dependence or population regulation with lags? *Nature* 344:660-663.
- VAN BALLEMBERGHE, V. 1987. Effects of predation on moose numbers: a review of recent North American studies. *Swedish Wild. Res. Suppl.* 1:431-460.
- _____, and W. B. BALLARD. 1994. Limitation and regulation of moose populations: the role of predation. *Can. J. Zool.* 72:2071-2077.