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Source: *Ecology*, Vol. 75, No. 2 (Mar., 1994), pp. 478-488

Published by: Ecological Society of America

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UNGULATE POPULATION MODELS WITH PREDATION: A CASE STUDY WITH THE NORTH AMERICAN MOOSE¹

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Abstract. In this article I examine moose–wolf interactions over a broad spectrum of moose densities with the primary objective to test empirically whether wolf predation can regulate moose numbers. I also present four conceptual models of moose population dynamics and outline their specific predictions. Based on 27 studies where moose were the dominant prey species, the functional and numerical responses of wolves to changing moose density were derived using an hyperbolic, Michaelis-Menten function. Per capita killing rate was strongly related ($P = .01$) to moose density, as was the density of wolves ($P < .01$). Killing rate plateaued at $3.36 \text{ moose} \cdot \text{wolf}^{-1} \cdot (100 \text{ days})^{-1}$ when predators were fully satiated. The asymptotic value for wolf density was $58.7 \text{ animals}/1000 \text{ km}^2$. Wolf predation rate, as derived from the total predator response, proved to be density dependent from 0 to $0.65 \text{ moose}/\text{km}^2$, and inversely density dependent at higher moose densities. Predator : prey ratios reflected wolf predation rate poorly because they did not integrate the functional response. An empirical model based on these results suggests that moose would stabilize at $2.0 \text{ moose}/\text{km}^2$ in the absence of predators, and at $\approx 1.3 \text{ moose}/\text{km}^2$ in the presence of a single predator, the wolf. Density-dependent food competition creates these two high-density equilibrium conditions. If moose productivity is diminished through either deteriorating habitat quality or bear-induced early calf mortality, then a low-density equilibrium ($0.2\text{--}0.4 \text{ moose}/\text{km}^2$) is predicted. The model also suggests that when a low equilibrium develops, a “predator pit” is absent or extremely shallow, thus arguing against the appropriateness of a predation–food two-state model. Further research on the density relationship of bear predation, on the effect of alternate prey on wolf total response, and on the regulatory impact of food competition at high moose densities, is required for a full understanding of moose demography.

Key words: food competition; models; moose; population dynamics; population stabilization; predation; predator pit; ungulate; wolf.

INTRODUCTION

The density of moose (*Alces alces*) in North America can be extremely variable, both among areas and over time (Crête 1987, Gasaway et al. 1992). This has prompted numerous studies with the objective to establish factors that may explain this variability (e.g., Gasaway et al. 1983, 1992, Messier and Crête 1985, Ballard et al. 1991). This approach has provided insights into proximate causes of mortality, but there is still no consensus as to which factors regulate moose populations (conflicting views in Messier and Crête 1984, 1985, Peterson et al. 1984a, Crête 1989, Messier 1991, Skogland 1991, Boutin 1992).

The interaction between natural mortality and population density constitutes the central element of any population model of ungulates (Caughley 1976). It is therefore surprising that comparatively few studies have actually documented the relationship between major sources of mortality, like food competition and predation, and density-dependent changes in key demographic parameters of moose populations (Messier 1989). Because most studies are short term in nature

(i.e., 3–5 yr), the density relationship of specific mortality agents may be better understood by analyzing findings from independent studies with comparable ecological conditions, but with differing moose densities.

A contentious issue in the literature of ungulates, and of mammals in general, relates to the role of predation in creating prolonged prey suppression (Pimlott 1967, Keith 1974, Erlinge et al. 1984, Erlinge 1987, Kidd and Lewis 1987, Newsome et al. 1989, Sinclair 1989, Sinclair et al. 1990, Skogland 1991, Pech et al. 1992). To assess if predation is causing low prey density, one needs to quantify the total response of predators to changing prey density. Conceptually, this response has been divided into two components: the *numerical* and the *functional response* (Solomon 1949). The numerical response summarizes changes in predator numbers with prey density, whereas the functional response describes how the number of prey consumed per predator varies with prey density. The *total response* (the product of numerical and functional responses) may cause predation rate to be density dependent at low prey densities and inversely density dependent (depensatory) at high prey densities (Holling 1959, Messier and Crête 1985, Fryxell et al. 1988). It

¹ Manuscript received 5 August 1992; revised 16 March 1993; accepted 19 May 1993.

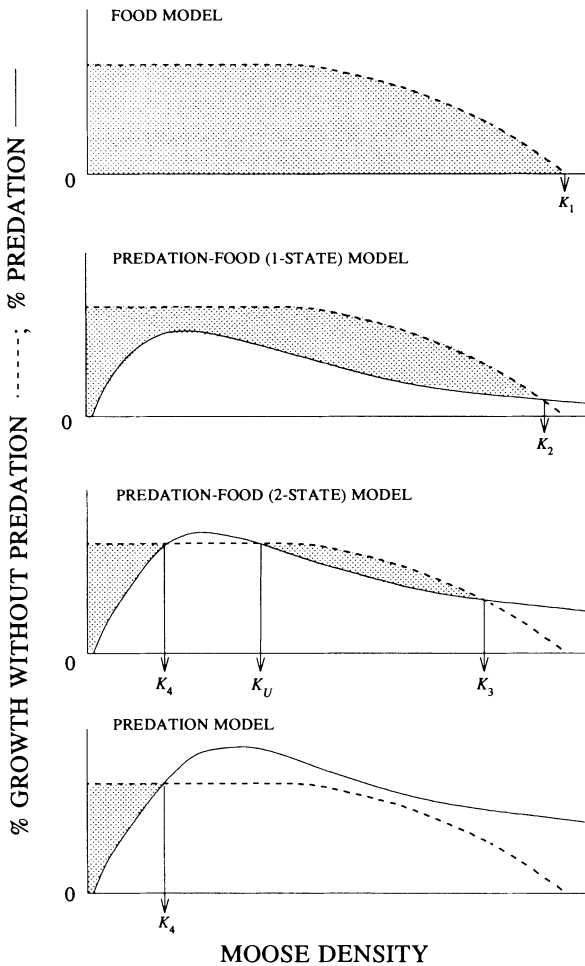


FIG. 1. Four conceptual models of ungulate population regulation (see *Some theory* for full explanation). The density relationship of wolf predation (—) and the growth rate of the prey without predation (---) are illustrated. When the two lines cross, an equilibrium condition is possible. K_1 to K_4 are stable equilibria, whereas K_U is dynamically unstable. The shaded area represents the net population growth rate after consideration of predation.

is of primary importance to assess the density relationship of predation if the objective is to develop population models able to predict ungulate population dynamics (Messier and Crête 1985, Van Ballenberghe 1987).

In this paper, I review wolf (*Canis lupus*) and moose interactions over a broad spectrum of moose densities. The primary objective is to test empirically whether wolf predation can regulate moose numbers. I also present four conceptual models of moose population dynamics and outline their specific predictions. Finally, I review the situations where wolf predation could explain the presence of a low population equilibrium at which moose may persist for extended periods of time at densities substantially below food-carrying capacity.

TABLE 1. Comparison of four models proposed to explain the population dynamics of large ungulates exposed to predation. Equilibrium densities (e.g., K_1) are depicted in Fig. 1.

Model	Prediction
1. FOOD	Ungulates are food-stressed at K_1 . Population growth rate would increase monotonically if the density of ungulates is lowered.
2. PREDATION-FOOD (one-state)	Ungulates are food-stressed at K_2 . Population growth rate would not increase monotonically if the density of ungulates is lowered. Predation is density dependent at low ungulate densities.
3. PREDATION-FOOD (two-state)	Ungulates are food-stressed at K_3 . Predation is density dependent at the lower range of ungulate density (below K_4). Ungulates are not food-stressed at K_4 . Predator removal would cause an immediate growth of an ungulate population regulated at K_4 , and, assuming an increase above K_U , the population will continue to grow up to K_3 after re-colonization by predators.
4. PREDATION	Predation is density dependent at the lower range of ungulate density (below K_4). Ungulate density will revert to K_4 after termination of a predator control program. Ungulates are not food-stressed at K_4 . Habitat improvement would not generate an escape of ungulates from heavy predation to high densities.

SOME THEORY

Predator-moose-vegetation dynamics can be depicted graphically (Fig. 1) to illustrate contrasting hypotheses of population regulation. The presentation of these hypothetical models is intended as an aid to conceptualize trophic interactions. Table 1 summarizes predictions associated with each model.

In a predator-free area, a moose population is expected to display logistic growth (FOOD model), resulting in a single, upper density equilibrium (K_1 in Fig. 1; Crête 1987, 1989). This equilibrium is called

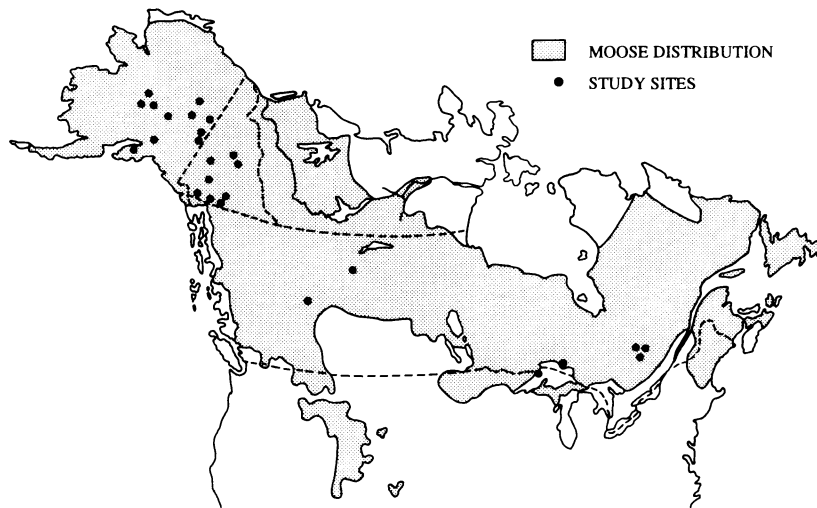


FIG. 2. Distribution of moose in North America (modified after Kelsall 1987) and study sites where moose–wolf interactions have been investigated.

the food-carrying capacity (KCC sensu Macnab 1985). Food competition constitutes the regulatory factor, which often exerts an accelerating depressive impact close to KCC (Caughley 1976, McCullough 1979, Skogland 1985, Fowler 1987, Dublin et al. 1990, Choquenot 1991, McCullough 1992). This FOOD model predicts that a population close to K_4 would exhibit general or age-specific malnutrition. Second, the population growth rate would increase monotonically if the density is lowered (due to human harvesting for example).

In the presence of predators, moose models may have three qualitative variants, although a continuum of possible outcomes exists depending on how effective predation is at reducing moose population growth (Messier and Crête 1985). In the PREDATION–FOOD one-state model (Fig. 1), predation reduces, in a density-dependent fashion, moose population growth at low densities, but never sufficiently to create a low equilibrium. The population, if not exploited, will tend toward a high equilibrium (K_2) where density-dependent food competition is regulating the population. This model predicts that moose are food-restricted at high density, and the population growth rate would not increase monotonically if the density is lowered. The latter prediction differentiates the PREDATION–FOOD one-state model from the FOOD model.

Assuming that the density relationship of predation is characterized by a density-dependent phase at low densities, and an inversely density-dependent phase at higher densities (Holling 1959, Messier and Crête 1985, Pech et al. 1992), the predator–prey system may be subject to a low-density equilibrium (K_1) and a high-density equilibrium (K_3 , Fig. 1). This PREDATION–FOOD two-state model results from density-dependent predation exceeding the potential rate-of-increase of moose at low–moderate densities, but a relaxation

of predation at higher densities allows for a positive population growth. Thus, a “predator pit” exists immediately above K_4 . If the moose can increase at a density above the predator pit (i.e., above K_1 in Fig. 1), then the moose population will stabilize at K_3 due to density-dependent food competition. The discriminating prediction of the PREDATION–FOOD two-state model is that a predator removal would cause an immediate growth of a moose population regulated at K_4 , and, assuming an increase above K_1 , moose will continue to grow up to K_3 after re-colonization by the predator.

If predation is quite effective at reducing moose population growth, moose may be maintained at low density due to density-dependent predation. This PREDATION model (Fig. 1) will result in a single low-density equilibrium (K_1) with limited possibility for moose to escape heavy predation. Thus, there is no “predator pit” associated with the PREDATION model. The discriminating prediction of this model is that moose density will revert to K_4 after termination of a predator control program. In addition, habitat improvement is unlikely to generate an escape of moose from heavy predation to high densities.

Data sources and analyses

I reviewed the literature for field studies on moose–wolf interactions in North America (Table 2, Fig. 2). I selected only studies where there was evidence that moose constituted the dominant prey species of wolves, here defined as >75% of the ungulate biomass consumed. Several important studies on “multi-prey systems” by Pimlott et al. (1969), Carbyn (1975, 1983), and Potvin (1988) were omitted from this analysis because the presence of a numerically important alternate prey may affect the predator response. Most selected studies were conducted in the northern coniferous for-

TABLE 2. Estimated moose densities, winter wolf density, killing rate (number of moose killed per 100 wolf-days), and pack size for moderately harvested wolf populations using moose predominantly as prey in various areas of North America.

Locations and year(s) of sampling	Moose density (no./km ²)	Wolf density (no./10 ³ km ²)	Killing rate [moose·wolf ⁻¹ ·(100 d) ⁻¹]	Pack size	Reference
Carmacks, Yukon, 1982	0.04	2.0	Gasaway et al. 1992
Dromedary Mountain, Yukon, 1982	0.06	10.0	Gasaway et al. 1992
East Alaska, 1981	0.09	8.0	Gasaway et al. 1992
Central Alaska, 1986	0.09	3.0	Gasaway et al. 1992
Aishihik, Yukon, 1981	0.11	3.0	Gasaway et al. 1992
East Alaska, 1987	0.12	4.5	Gasaway et al. 1992
Nisutlin, Yukon, 1986	0.13	10.0	Gasaway et al. 1992
Mayo, Yukon, 1988	0.14	10.0	Gasaway et al. 1992
East Alaska, 1990	0.14	9.0	Gasaway et al. 1992
South-central Yukon, 1983	0.15	13.0	Gasaway et al. 1992
Southwest Québec, 1980–1984	0.17	3.6	0.37	3.0	Messier 1985, Messier and Crête 1985
Central Alaska, 1976	0.18	15.6	...	9.3	Gasaway et al. 1983
Central Alaska, 1986–1987	0.19	6.0	Gasaway et al. 1992
Central Alaska, 1980	0.19	8.0	Gasaway et al. 1992
Central Alaska, 1986	0.19	15.0	Gasaway et al. 1992
East Denali National Park, Alaska, 1984	0.22	5.9	...	5.3	Singer and Dalle-Molle 1985, Singer 1987
Southwest Québec, 1980–1984	0.23	8.2	0.47	3.7	Messier 1985, Messier and Crête 1985
Northeast Alberta 1975–1978	0.23	11.1	1.90	6.8	Fuller and Keith 1980
South-central Yukon, 1983	0.26	11.8	2.04	8.4	Larsen et al. 1989, Hayes et al. 1991
East Denali National Park, Alaska, 1966–1974	0.27	12.7	...	7.5	Singer and Dalle-Molle 1985, Van Ballenberghe 1987
Northwest Ontario, 1975–1979	0.30	11.9	Bergerud et al. 1983
South-central Alaska, 1975*	0.33	10.3	2.78	11.0	Ballard et al. 1987, Ballard et al. 1991
Southwest Québec, 1980–1984	0.37	14.8	1.12	5.7	Messier 1985, Messier and Crête 1985
Teslin burn, Yukon 1984	0.42	18.0	1.74	7.1	Hayes and Baer 1986, Gasaway et al. 1992
Kenai Peninsula, Alaska, 1976–1982	0.80	14.2	1.85	10.5	Peterson et al. 1984b
Isle Royale, 1959–1960	1.00	38.6	...	9.5	Mech 1966, Jordan et al. 1967, Peterson and Page 1988
Isle Royale, 1976–1980	1.11	77.6	1.88	7.5	Peterson and Page 1988
Isle Royale, 1961–1965	1.20	43.8	...	7.9	Mech 1966, Jordan et al. 1967, Peterson and Page 1988
Northwest Alberta, 1979–1980	1.30	22.1	1.96	6.0	Bjorge and Gunson 1989
Isle Royale, 1981–1985	1.37	41.5	1.80	5.6	Peterson and Page 1988
Isle Royale, 1971–1975	1.41	51.1	2.44	7.3	Peterson 1977, Peterson and Page 1988
Isle Royale, 1966–1970	1.73	36.3	2.81	4.9	Jordan et al. 1967, Peterson and Page 1988, Wolfe and Allen 1973
Isle Royale, 1986–1990	2.49	26.0	3.75	4.2	Peterson and Page 1988, R. O. Peterson, unpublished manuscript

* The moose density in 1975 was estimated at 50% of the 1980 density based on changes in number of moose seen per hour of survey (Ballard et al. 1991); killing rate was quantified in 1979–1980 when moose density was 0.66 animal/km².

est where moose were the predominant ungulate species.

Four parameters were analyzed: moose density, wolf density, per capita killing rate, and pack size. All parameters were assessed in winter when moose and wolves could be observed from aircraft. To avoid systematic biases, the following rules were adopted:

1. For studies involving a wolf control program, the wolf density before reduction was selected;
2. When the author presented annual estimates for a given parameter, the unweighted mean was used;
3. Data originally presented as a range, or as two separate estimates (e.g., early and late winter wolf density) have been averaged to a single figure;

4. Average pack size included pairs, but not singles.

For each study, except for Isle Royale, only one estimate per parameter was used in this analysis. For Isle Royale, the data set was subdivided into 5-yr periods and each subset was treated independently. This data arrangement was required because the Isle Royale study has been ongoing for more than 30 yr, with pronounced changes in moose and wolf density (Peterson and Page 1988). These estimates may be partly dependent even if they were calculated every 5 yr, but it was judged that this problem was less of a concern than pooling data over a 30-yr period.

The functional response of wolves was determined by the hyperbolic, Michaelis-Menten function, an equation mathematically equivalent to the Holling's disk equation (Real 1977). The equation takes the form $y = ax/(b + x)$, where y is the per capita killing rate and x is the moose density. In addition, 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 above formulation describes a Type II functional response. The equation can be extended to a Type III functional response by simply adding an exponent to the parameter x (Real 1977). Both types of equations were fitted to the data with a Marquardt-Levenberg algorithm (a least-squares technique; Press et al. 1986). Curve fitting was performed with the software Table Curve, Version 3.1 (Jandel Scientific, Corte Madera, California). Statistical testing of the model was based on the coefficient of multiple determination (Sokal and Rohlf 1981:631–632).

The numerical response of wolves was calculated by a modified Michaelis-Menten function (Fryxell 1991) which took the form $y = a(x - c)/(b + (x - c))$. Here, y is the density of wolves and c is the density of moose at which wolf density should be nil. This formulation takes into account the possibility that a threshold of moose density exists below which wolves cannot subsist (Messier and Crête 1985). Other parameters are as defined above. The same least-squares technique was used to estimate parameters of the equation.

I determined the proportional effect of the functional and numerical responses to assess their contribution to changes in predation rate. The proportional effect was calculated by dividing the rate of increment of each type of response by half the rate of increment of moose density (full method described in the Appendix). Values greater than unity imply a density-dependent predation rate because the predator response grows faster than prey numbers. Values lower than unity indicate an inversely density-dependent function.

RESULTS

Information from 27 studies was available to analyze the pattern of wolf predation with changing moose density (Table 2). Variation in moose density reflected, to a large extent, differences in the abundance and com-

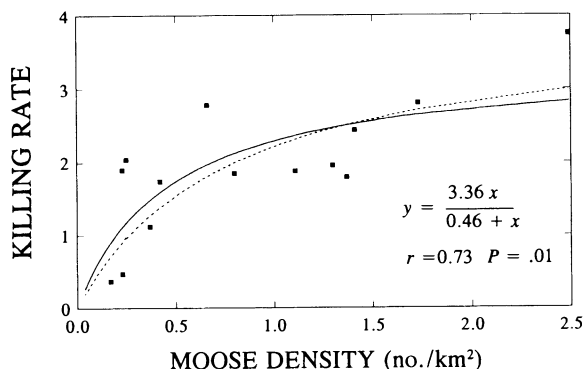


FIG. 3. The functional response of wolves to changing moose density. Killing rate (number of moose killed per wolf per 100 days) was related to moose density with a hyperbolic, Michaelis-Menten equation. The dashed line refers to an independent analysis after exclusion of the data obtained below 0.3 moose/km².

position of large predators in each region, and the history of human hunting. Consequently, the presence of predators other than the wolf, e.g., black bear (*Ursus americanus*) and grizzly bear (*U. arctos*), and differing hunting pressure were considered here as manipulative agents that potentially reduced moose populations below their upper, food-regulated density. The response of wolves to differing moose densities was then quantified using inter-population analyses.

Functional response

The functional response of wolves to changes in moose density is shown in Fig. 3. The killing rate proved to be related to moose density (Michaelis-Menten model, $r = 0.73$, $df = 12$, $P = .01$). A Type III functional response of the general form $y = bx^c/(a + x^c)$ (Real 1977), where y is the killing rate and x represents moose density, did not improve the fit (best model, $c = 1$, $r = 0.73$). The killing rate increased rapidly at low moose densities (Fig. 3) and reached an asymptotic value of 3.36 ± 0.67 moose · wolf⁻¹ · (100 days)⁻¹ (mean ± 1 SE) indicating predator satiation. The moose density associated with half the maximum killing rate was 0.46 ± 0.26 moose/km².

Killing rates were especially variable below 0.3 moose/km² (Fig. 3), ranging from 0.37 to 2.04 moose · wolf⁻¹ · (100 days)⁻¹. An independent analysis was performed, after exclusion of these data, to test the robustness of the functional response. The new Michaelis-Menten function ($y = 3.92x/0.77 + x$) was significant at $P = .08$ ($r = 0.69$, $df = 8$). Considering that there were no a priori reasons to exclude these data, and that the new equation parameters had minimal effects on the functional response (see Fig. 3), the original function was retained for estimating predation rate (below).

A possible relationship between mean pack size and killing rate was explored by an analysis of residual values (ANCOVA). If pack size creates an independent

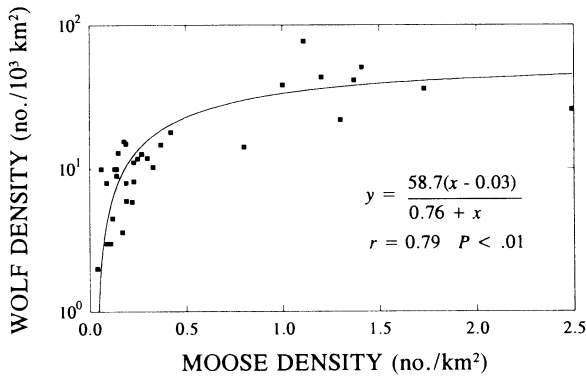


FIG. 4. The numerical response of wolves to changing moose density. Wolf density (presented on a log₁₀ scale) was related to moose density with a hyperbolic, Michaelis-Menten equation.

effect on killing rate, I would predict that residual values along the regression line (Fig. 3) would be related negatively to pack size (i.e., members of large packs may realize lower per capita killing rate). However, a linear regression using residual values revealed that mean pack size was not an independent explicative variable of killing rate ($r = 0.15, P > .20$).

Numerical response

Wolf density was clearly a function of moose density as revealed by the modified Michaelis-Menten model ($r = 0.79, df = 29, P < .01$). The numerical response showed a sharp increase at low moose densities (Fig. 4) and plateaued at 58.7 ± 18.6 wolves/1000 km² (mean ± 1 SE). The moose density at half the maximal wolf density was estimated at 0.76 ± 0.61 moose/km². The moose density below which wolves were absent was only 0.03 ± 0.07 moose/km². A general Type III numerical response, as described above, did not appreciably improve the fit (best model, $c = 1.6, r = 0.80$ vs. 0.79).

Total response and predation rate

The total response reveals the absolute number of kills per unit time. Predation rate can be calculated as (total response $\times 0.365$) \div (moose density). The constant 0.365 is required to compute the year-long predation rate. From 0 to 0.65 moose/km², predation was strongly density dependent (Fig. 5). Above 0.65 moose/km², predation rate gradually declined (Fig. 5). The numerical and the functional response did not contribute equally to changes in predation rate. At low moose densities, the numerical response was the principal factor underlying density dependence (Fig. 5). At high moose densities, the functional response was comparatively more important in creating the depensatory, destabilizing impact of predation.

The predator-prey ratio was investigated as an index of wolf predation rate. The number of wolves per 100

moose peaked at 0.18 moose/km² and gradually declined at higher moose densities. Changes in predator-prey ratios did not reflect variations in predation rate (Fig. 5). The ratio estimator peaked at a moose density substantially lower than the one specific to predation rate (0.18 vs. 0.65 moose/km²). In addition, the depensatory trend of wolf: moose ratios was more pronounced than the trend documented for the predation rate (Fig. 5).

Scaling of the model

Two types of scaling are required to build a realistic population model based on the above results. First, one needs to re-scale the predation rate (Fig. 5) because winter killing rates may not reflect accurately the frequency at which wolves prey on moose on a year-long basis. The most complete data set to make a proper re-scaling was summarized by Messier and Crête (1985) for their "high" density area (0.37 moose/km²). There, the year-long wolf predation rate was estimated at 19.3%, compared to a predicted predation rate of 27.3% as calculated from the total wolf response (Fig. 5). Con-

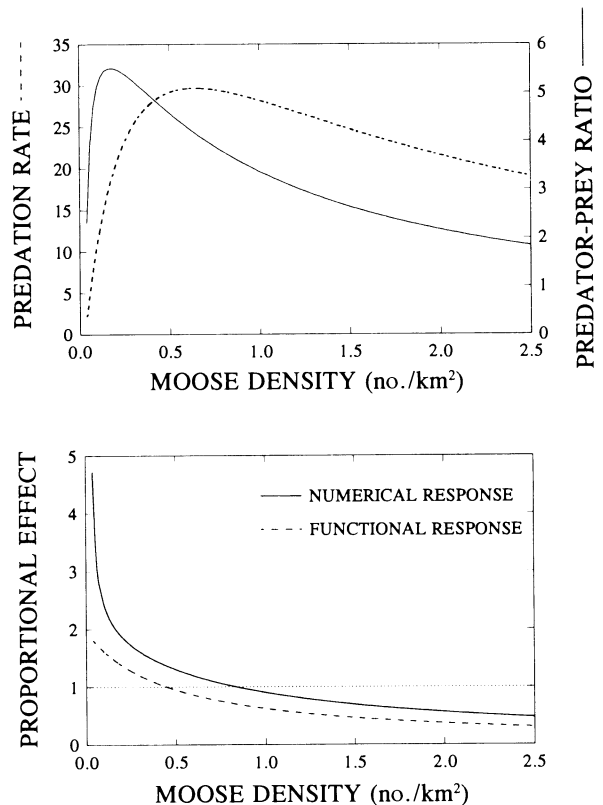


FIG. 5. Changes in wolf predation rate (as calculated from the total response) with moose density showing a density-dependent response up to 0.65 moose/km², followed by an inversely density-dependent response. The ratio of number of wolves per 100 moose (an index of predation rate) is also presented. The proportional effects of the functional and numerical responses on predation rate are presented in the lower panel (see the Appendix for calculation).

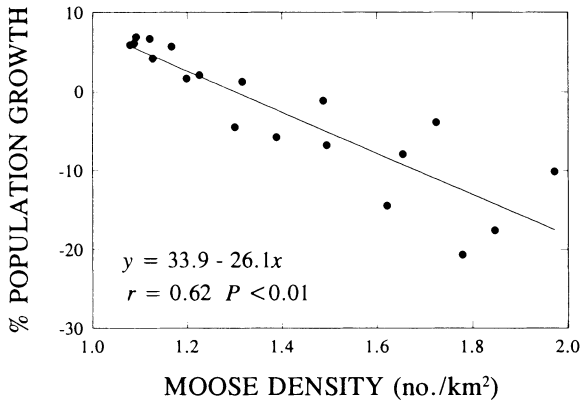


FIG. 6. Changes in moose population growth with increasing moose density at Isle Royale after statistically controlling for the effect of wolf predation. The declining response was assumed to reflect food competition (after Messier 1991).

sequently, a correction factor of 0.71 was applied to predation rate values. Note that the correction factor does not alter the trend of the predation rate, only its general elevation.

Second, predation rate needs to be compared to the rate of increase of moose populations not subject to predation. Recently, Fryxell (1988) reviewed the population dynamics of moose in Newfoundland where wolves and grizzly bears were absent. He concluded that moose populations can sustain a maximum harvest rate of 25%. This maximum rate of increase was comparable to estimates reported by other researchers (Keith 1983, Van Ballenberghe 1983) and was assumed in the present population model. Food competition must depress population growth at high moose densities, although this relationship is poorly documented. At Isle Royale, population growth declined with moose density when moose abundance exceeded 1 animal/km² (Fig. 6; Messier 1991). A comparable decline (slope = -26.1) was assumed here.

The empirical data summarized above suggest that in the presence of a single predator, the wolf, moose would stabilize at ≈ 1.3 moose/km², compared to an equilibrium density of 2.0 moose/km² with no predators (curve 1, Fig. 7). Both high-density equilibria are caused by density-dependent food competition. If moose growth rate is reduced by only 5–10%, because of either a less productive habitat or a density-invariant predation rate by an alternate predator like grizzly or black bear, then a low-density equilibrium is predicted (Curve 2 and 3, Fig. 7). This low equilibrium is the result of density-dependent predation rate by wolves. The most striking feature of the model is the fact that a multiple-equilibrium system is practically impossible to generate; as soon as a low equilibrium is apparent, the high equilibrium disappears (curve 2, Fig. 7). The model suggests that a "predator pit" is either absent or extremely shallow, and, therefore, ineffective in cre-

ating a low-density equilibrium. This implies that the low equilibrium is consistent with the PREDATION model, not the PREDATION-FOOD two-state model.

DISCUSSION

The present study suggests that wolf predation can be strongly density dependent at the lower range of moose density. This result contrasts with the conclusion of Sinclair (1989), Skogland (1991), and Boutin (1992) who stated that there is no evidence that predation is capable of regulating ungulates. I would like to note, however, that Sinclair (1989) and Skogland (1991) did not perform an exhaustive analysis among populations as in this study. Also, Boutin (1992) assessed the density dependence of wolf predation on moose, but without partitioning the numerical and the functional responses.

Predation rate is undoubtedly a response to a variety of factors beyond the first-order influence of moose density. Factors that may have obscured the density relationship of wolf predation include differences in alternate prey species, body size variation of wolves among areas, and variation in methodology among studies. Considering that the above variables could not be accounted for in the calculation, and yet the functional and numerical responses were statistically related to moose density at $P \leq .01$ (Figs. 3 and 4), I conclude that the density relationship of wolf predation is qualitatively "robust," particularly the density-dependent portion of the curve at low moose densities. At densities > 1.0 moose/km², data were largely from Isle Royale, a closed ecosystem. Consequently, the compensatory portion of the curve, and the predicted high-density equilibria (K_1 and K_2), should be interpreted qualitatively.

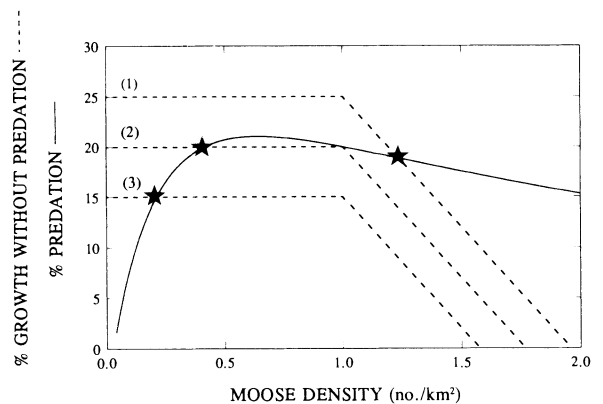


FIG. 7. Empirical model of moose-wolf dynamics as derived from field data on wolf predation rate (—) and moose population growth without wolf predation (---). Models 1, 2, and 3 illustrate possible stable equilibrium conditions (★) when the productivity level of moose is reduced by either deteriorating habitat quality or bear-induced calf mortality.

Why is wolf predation so effective in reducing moose population growth at low densities? Moose are non-gregarious (Geist 1963), are well distributed in their environment, and show limited seasonal migration (Van Ballenberghe and Peek 1971, Phillips et al. 1973, Addison et al. 1980). Seasonal aggregation of prey may reduce predation risk (Messier and Barrette 1985) and migration may confer important benefits in terms of safety against predators (Fryxell et al. 1988, Messier et al. 1988). Thus, because moose are well dispersed in their environment, and spatially predictable, they are well exposed to wolf predation and always part of the year-long prey base. At low moose density, wolves, being obligate predators of ungulates (Mech 1970), must persist in exploiting moose if other ungulates are rare or seasonally absent.

Wolf: ungulate ratios have been proposed as an indicator of the impact of wolf predation (Gasaway et al. 1983, Keith 1983, Fuller 1989). Yet in the present study wolf: moose ratios poorly reflected predation rate. For example, wolf: moose ratios peaked at a density about $\frac{1}{4}$ of the one predicted by the total response (Fig. 5). The ratio estimator also suggested an inversely density-dependent impact of predation which was much more pronounced than the decline in predation rate at high moose densities. This poor correspondence is explained by the fact that the ratio estimator does not include consideration of the functional response (Messier and Crête 1985). Theberge (1990) discussed other important limitations of predator: prey ratios.

Recent studies by Franzmann et al. (1980), Stewart et al. (1985), Franzmann and Schwartz (1986), Boertje et al. (1988), Larsen et al. (1989), and Ballard et al. (1991) have demonstrated that grizzly and black bears may be important predators of moose calves in summer. Because bear predation affects primarily the first age class and for only a short period in summer, but wolf predation does impact all age classes year-round, it is expected that predation by wolves would exceed the limiting effect of bear predation (Hayes et al. 1991). The key element, however, is whether bear predation on moose calves is density dependent. Schwartz and Franzmann (1991) and Ballard (1992) concluded after reviewing the empirical evidence that bear predation appeared to be independent of moose density. The implication of this in terms of moose population dynamics is nonetheless important. A predator that removes a constant proportion of calves independent of moose density can shift the system from a high equilibrium to a low equilibrium condition (e.g., compare curves 1 and 3 in Fig. 7). Messier and Crête (1985), Crête (1987), Van Ballenberghe (1987), and Gasaway et al. (1992) stressed that the presence of a second predator would favor a low-density equilibrium (i.e., a shift from a PREDATION-FOOD one-state system to a PREDATION system). This postulated change with the addition of a second predator also illustrates

that a density-independent limiting factor, possibly one such as bear predation, can dramatically shift the density at which an equilibrium condition occurs even if not a regulatory process in itself (Sinclair 1989).

The impact of predation at the population level must include consideration of the total predator response, but also the breeding potential of the prey, which for moose is known to change with forest succession and habitat quality (Franzmann and Schwartz 1985, Albright and Keith 1987). An impoverishment of habitat quality may gradually shift the system from a high equilibrium to a low equilibrium condition, even if the density relationship of wolf predation remains unchanged. The empirical model presented in Fig. 7 predicts that moose populations inhabiting relatively unproductive habitats (e.g., mature forests, northern taiga), are prone to be regulated at low densities due to density-dependent wolf predation (i.e., PREDATION model).

The empirical model developed here does not support the appropriateness of a PREDATION-FOOD two-state model for moose. The critical elements to generate a multi-equilibrium scenario is a rapidly increasing predation rate at extremely low prey densities, and a substantial relaxation of predation at elevated prey densities. For moose, the low equilibrium occurs within the range of 0.2–0.4 moose/km², or $\approx 1/4$ to $1/10$ of KCC. For the only other ungulate system for which a multi-equilibrium system has been suggested, i.e., nonmigrant ungulates in eastern Africa (Fryxell et al. 1988), the low equilibrium develops at only 1.5% of KCC. The rather weak compensatory nature of wolf predation (Fig. 7) probably precludes the formation of a high-density equilibrium for moose populations cohabiting with at least two species of predators, or inhabiting a relatively poor habitat. Considering that most moose populations cohabit with at least two species of predators in North America, it is not surprising to observe that lightly exploited moose populations are found almost without exception at low densities compared to KCC (Crête 1987, Van Ballenberghe 1987, Gasaway et al. 1992). The Isle Royale moose population, a notable exception, is associated with only one predator species. For such cases, the model (Fig. 7) predicts high moose densities maintained by food competition, with potentially recurring fluctuations if a time lag effect is considered (Peterson et al. 1984a, Messier 1991). At high moose densities, wolves limit, but do not regulate, moose numbers (Messier 1991).

Little information exists on the influence of alternate prey on moose-wolf interactions. Theoretically, one can postulate two outcomes with opposite effects. First, an increase in alternate prey could decrease predation on the primary prey by dilution of the functional response, particularly if the alternate prey is preferred by the predator (Real 1979). For example, the presence of an ungulate species with a higher degree of vulner-

ability than moose, like white-tailed deer (*Odocoileus virginianus*) and wapiti (*Cervus elaphus canadensis*), may dilute wolf predation and allow for a greater abundance of moose than otherwise expected. Studies by Pimlott et al. (1969), Carbyn (1983), and Potvin (1988) support this interpretation. Second, the presence of an alternate prey may increase predation by promoting a favorable numerical response. Gates and Larter (1990) have proposed that the recent eruption of wood bison (*Bison bison athabascae*) in the Mackenzie Bison Sanctuary, Northwest Territories, may exacerbate predation on moose, rather than diverting it. Here, the increase in bison appears to favor higher wolf abundance, although wolves probably exploit moose preferentially. An analogous situation has been described by Bergerud and Elliot (1986), Edmonds (1988), and Seip (1992) with regard to the decline of woodland caribou (*Rangifer tarandus*) with expanding moose populations within the range distribution of woodland caribou. Evidently, more research is required to fully understand the implication of alternate prey on moose population dynamics when predation operates. It seems clear, however, that the relative vulnerability of the primary vs. the alternative prey to predation plays a determining role in creating either a diluting (via changes of the functional response) or an exacerbating (via changes of the numerical response) impact on the abundance of the primary prey.

There is now a good theoretical and empirical understanding of the effect of wolf predation on moose population dynamics. In fact, the documented functional and numerical responses of wolves to changing moose density is unique in the mammalian literature. Research on the density relationship of bear predation, on the effect of alternate prey on wolf total response, and on the regulatory impact of food competition at high moose density, is nonetheless required before a full understanding of moose demography can be claimed.

ACKNOWLEDGMENTS

The Natural Sciences and Engineering Research Council of Canada supported my work through a University Research Fellowship and an operating grant for computer analyses. I would like to thank all of those who sweated (or froze) in the field studying wolf predation on moose; without their remarkable effort this analysis would not have been possible. I appreciate the helpful and constructive comments on the manuscript provided by S. Boutin, M. Crête, S. Erlinge, B. R. Neal, R. O. Peterson, M. A. Ramsay, and M. K. Taylor.

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APPENDIX

The proportional effect of the functional and the numerical response was computed by comparing the rate of increment of each response to the rate of increment of prey density. Writing prey densities as D_1, D_2, \dots, D_m , predicted predator densities as P_1, P_2, \dots, P_m , and predicted killing rates as K_1, K_2, \dots, K_m , the proportional increment for prey density, predator density, and killing rate can be calculated as follows:

$$d_i = \log_e(D_{i+1}/D_i)$$

$$p_i = \log_e(P_{i+1}/P_i)$$

$$k_i = \log_e(K_{i+1}/K_i)$$

The proportional increment of the total predator response, r_i , is given by $p_i + k_i$, considering that the total predator response is the product of the functional and numerical responses.

Therefore, predation rate must be density dependent if $r_i > d_i$, and inversely density dependent if $r_i < d_i$. Assuming an equal contribution of each type of response, the condition for density dependence is reduced to $p_i > 0.5 d_i$ or $k_i > 0.5 d_i$.

The proportional effect of the numerical and the functional response was then defined as $p_i/(0.5 d_i)$ and $k_i/(0.5 d_i)$, respectively. The proportional effect here simply illustrates how the rate of increment of each type of response compares to the rate of increment of prey density for the purpose of judging density dependence. A value greater than unity would tend to create a density-dependent function, and a value smaller than unity would generate an inversely density-dependent function. This formulation was adopted in calculating data presented in Fig. 5 (lower panel), using moose density increments of 0.02 moose/km².