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Applying difference equations to wolf predation

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Abstract: Parameters for generalized Lotka–Volterra equations, expressed as difference equations, have been estimated from actual data on wolves and their prey. The functional response is represented by a single constant, while the numerical response is expressed as a ratio-dependent limitation on predator abundance. Parameters for the Lotka–Volterra equations were estimated by multiple-regression fits to data on moose (*Alces alces*) and wolves (*Canis lupus*) on Isle Royale, and from other sources. Observed prey–predator ratios are highly variable, but much of the variability may arise from nonequilibrium conditions. A multiple-prey model has been developed by assuming that utilization rates vary in proportion to relative current biomass. If analyses are to be useful, the dynamic, nonlinear nature of predator–prey systems requires that a system of equations be developed, along with extensive series of observations of actual abundances of predator and prey.

Résumé : Les paramètres utilisées dans les équations généralisées de Lotka–Volterra, exprimées sous forme d'équations aux différences finies, ont été estimés à partir de données réelles sur des loups et leurs proies. La réponse fonctionnelle est une simple constante, alors que, dans la réponse numérique, l'abondance des prédateurs dépend du rapport prédateurs–proies. Les paramètres des équations de Lotka–Volterra ont été estimés par l'ajustement de régressions multiples à des données sur des Orignaux (*Alces alces*) et des Loups gris (*Canis lupus*) d'Isle Royale et d'autres endroits. Les rapports proies–prédateurs observés se sont avérés très variables, mais cette variabilité peut provenir de conditions de non-équilibre. Un modèle à proies multiples basé sur l'hypothèse selon laquelle les taux d'utilisation varient en fonction de la biomasse relative du moment a été mis au point. La nature dynamique, non linéaire, des systèmes prédateurs–proies nécessite un système d'équations pour fin d'analyses appropriées, de même que des séries de données réelles d'abondance de prédateurs et de proies.

[Traduit par la Rédaction]

Introduction

Predator–prey equations have been the subject of considerable interest in ecology since the 1920s, but for the larger vertebrates, much of the treatment has been theoretical, with little attention given to applications. A good deal of attention has been paid recently to ratio-dependent predator–prey interaction theory (Matson and Berryman 1992; Akcakaya et al. 1995; Abrams 1994; Berryman et al. 1995; Gleeson 1994; Sarnelle 1994), but the examples and experimental tests consider invertebrates, as does most of the theoretical work on the subject. There has also been much recent interest in issues concerning wolf predation in Alaska and Canada, but I have found it very difficult to examine the issues substantively (Eberhardt and Pitcher 1992). This stems in part from the usual problems with obtaining satisfactory data, but the limitations have been exacerbated by the need to deal with a dynamic system with interacting components.

Many wildlife problems can be approached with single-species models, and there is often sufficient stability to permit the use of linear (or log-linear) models (Eberhardt 1987). Quite straightforward statistical analyses then become possible, and the underlying models may not need or receive much attention. Predator–prey situations require nonlinear models and may be highly dynamic. Outcomes of changes, then, cannot be predicted using the kind of logical analysis that we might apply to single-species situations, and it is not reasonable to construct a conceptual model of possible outcomes in terms of the likely behavior of one of the interacting predator and prey species.

Consequently, while we may regard the well-known Lotka–Volterra system of equations as overly simplistic and thus unrealistic, it may nonetheless be valuable to look at the problems involved in trying to estimate parameter values for these models by using actual data. With computer simulations now widely used, the objection may be made that there is no need to work with oversimplified models. This may well be true. My experience in building computer models is that one has to make so many arbitrary decisions in order to construct a detailed model that it soon becomes impossible to make any kind of logical assessment of the outcomes of running the model. If a simple model fails to match reality, one can usually identify the weak points. Perhaps all that can be expected of such a model, however, is that it provides a “caricature” of the real world (May et al. 1979). If we can identify such a general correspondence between model outcomes and observed data, it may then become possible to capture and improve the correspondence in a more detailed model. The purpose of the present paper

is to evaluate a version of the Lotka–Volterra model that can be applied to actual data, and to emphasize some aspects which need further attention.

Methods and results

Basic equations

The equations considered here are generalized forms of the Lotka–Volterra equations, but are more appropriately expressed as difference equations (Eberhardt 1987, 1997). Most of the recent literature identifies two components, the “functional response,” referring to removals from the prey population by predators, and the “numerical response” of predators to prey abundance. A list of potential forms of these two functions was given by May (1981). The notation and basic equations used here are those given by Eberhardt (1997). The prey equation is

$$[1] \quad V_t = V_{t-1} + r_1 V_{t-1} \left[1 - \left(\frac{V_{t-1}}{K} \right)^z \right] - cH_{t-1}$$

where V_t denotes ungulate prey abundance at time t , H_{t-1} denotes predator abundance the previous year, K is the asymptotic population level of the prey, z is a constant for the generalized logistic equation (Eberhardt 1987), r_1 is the maximum rate of increase of prey, and c is the predation rate (number of prey taken per wolf each year). The predator equation is

$$[2] \quad H_t = H_{t-1} + r_2 H_{t-1} \left(1 - \frac{H_{t-1}}{aV_{t-1}} \right)$$

where r_2 is the maximum rate of increase of predators and a denotes the predator “equilibrium ratio,” i.e., the number of prey required to support one predator under equilibrium conditions.

The difference equations used here are easily implemented in any of the several computer “spreadsheets.” In plotting graphs of the outcomes, it is convenient to have the equilibrium values for eqs. 1 and 2. These are readily obtained by setting $H_t = H_{t-1}$ and $V_t = V_{t-1}$ and solving the resulting equations. This gives

$$[3] \quad V = K \left(1 - \frac{ca}{r_1} \right)^{1/z}, \quad H = aV$$

and the ratio at equilibrium is

$$\frac{H}{V} = a$$

Functional response

The essential feature of the functional response is the per capita consumption of prey by predators, which is here expressed as a constant, c (Eberhardt 1997). The main form in recent literature of a more elaborate function is the Michaelis-Menton equation used by Holling (1965) and thus widely known as Holling's disk equation.

Numerical response

In eq. 1, in the absence of predators, the prey are limited by a logistic function. The numerical response of predators to prey abundance is furnished with a similar function, devised by Leslie (1948), so the numerical response can be written as

$$[4] \quad \frac{H_t}{H_{t-1}} = \lambda_{t-1} = (1 + r_2) - \frac{r_2}{a} \left(\frac{H_{t-1}}{V_{t-1}} \right)$$

but in this case, the asymptotic value, K , becomes aV_{t-1} , i.e., it is proportional to the current abundance of prey, and r_2 is the rate of increase approached by predators when their numbers are low and prey are very abundant. Given estimates of the current rate of increase (λ_{t-1}), and the predator-prey ratio, the right side of eq. 4 can be fitted by linear regression, with the intercept estimating $\lambda = 1 + r_2$ and the slope r_2/a . Keith (1983) gave data that can be used in this fashion (Fig. 1).

Isle Royale data

Dr. R.O. Peterson (personal communication) has kindly made available unpublished wolf and moose data for Isle Royale. Inasmuch as these data represent one of the longest series available on moose and wolves, they provide a basis for studying curves using the above parameters. One approach is via multiple regression. Equations 1 and 2 can be rearranged to show how parameters are grouped in a multiple-regression fit:

$$[1] \quad V_t = (1 + r_1) V_{t-1} - \left(\frac{r_1}{K^2} \right) V_{t-1}^{s+1} - cH_{t-1}$$

$$[2] \quad H_t = (1 + r_2) H_{t-1} - \left(\frac{r_2}{a} \right) \frac{H_{t-1}^2}{V_{t-1}}$$

The multiple-regression equations are constrained to have zero intercepts, e.g., eq. 2 is $y = b_1x_1 + b_2x_2$ with

$$y = H_t, \quad x_1 = H_{t-1}, \quad x_2 = \frac{H_{t-1}^2}{V_{t-1}}, \quad b_1 = 1 + r_2$$

and $b_2 = \frac{r_2}{a}$

The multiple regressions (Fig. 2) are highly significant (analysis of variance, $P < 0.0001$), with all coefficients highly significant ($P < 0.01$), but the coefficients have larger standard errors (given in parentheses below) than might be desirable. However, it is interesting to compare the coefficients with the estimates from other sources. For the wolf data we get $b_1 = 1 + r_2 = 1.255$ (standard error = 0.10). The value estimated for b_2 gives an estimate of a from $b_2 = r_2/a = 9.105(3.02)$ and $a = 0.255/9.105 = 0.028$ wolves per moose, or 36 moose per wolf, giving $6(36) = 214$ deer-equivalents, compared with $a = 0.476/0.054 = 8.8$ wolves per 1000 deer-equivalents or 114 deer per wolf for Keith's data (Fig. 1). For moose, $b_1 = 1.217(0.055)$, so $r_1 = 0.217$. The second coefficient (b_2) in-

volves K and z , and likely cannot realistically be interpreted (z was arbitrarily set equal to 5.0 on the basis of earlier studies (Allen 1980; Eberhardt 1987)). The value of 6.32(2.36) for the third coefficient is presumably an estimate of the number of moose taken per wolf each year (the predation rate). Eberhardt (1997) estimated 6.9 moose per wolf each year from data in the literature.

The use of difference equations as the basis for the multiple-regression model results in an apparent lag of 1 year between model outcome and data points (Fig. 2). This is, at least partially, a consequence of compressing the events of birth and death into a single interval, as is necessary in using the difference equations here.

Prey-predator ratios

Two extensive tabulations of data on ratios of prey to wolves are those of Fuller (1989, Appendix B) and Messier (1994, Table 2). Fuller gave the prey abundance in deer-equivalents per 1000 km² and gave data on various prey species, whereas Messier reported only data on moose. These data were analyzed by Eberhardt (1997) and showed no evidence of curvilinearity or significant y -axis intercepts. The two sets of data are pooled here (6 cases of evident duplication of Messier's tabulation with data given by Fuller have been dropped). The multiple-regression estimate of 214 deer-equivalents from the Isle Royale data agrees well with the pooled data (204 deer-equivalents) from Fuller and Messier, so the major discrepancy is with the estimate from Keith's (1983) data. Because ratios of variable quantities are difficult to deal with by means of the usual statistical methods, bootstrapping (Efron and Tibishirani 1993) was used to compare the pooled results of Fuller and Messier with the estimate from Keith's data.

Because the regression data (Fig. 1) from Keith (1983) are based on only 7 observations, "parametric" bootstrapping was used to assess this data set. Deviations from regression were randomly sampled with replacement, and corresponding values of the independent variable were computed for each of 2000 such samples to give percentile confidence limits (Efron and Tibishirani 1993). The larger pooled data set ($n = 53$) from Fuller (1989) and Messier (1994) was assessed directly by means of "nonparametric" bootstrapping. That is, 53 random samples with replacement were taken for each "bootstrap sample" and the pooled ratio was calculated. The frequency distributions from the two data sets did not overlap at all, making it evident that two different underlying values are involved. Approximate 95% confidence limits for the pooled value (204 deer-equivalents) were 173-278, while the 95% limits for the estimate from Keith's data (114 deer-equivalents) were 88-136.

Steady-state models

Gasaway et al. (1992, Fig. 12), following Messier and Crete (1985), proposed that moose populations might attain several distinct equilibrium population levels under wolf predation. They also reported (Gasaway et al. 1992, Fig. 13) large differences in actual moose densities between areas where predators (wolves and bears) were likely limited by harvesting and areas where they were lightly harvested. Messier (1994, Fig. 1) proposed similar conceptual models that showed very different steady-state levels for moose preyed on by wolves. However, he did not propose specific equations for the hypothesized

Fig. 1. Annual rates of increase in the wolf population at various values of the ratio of wolf numbers to prey abundance. Data are from Keith (1983, Tables 1 and 3). The standard error of the slope of the regression line is 0.011 and the standard error of the intercept is 0.041. The regression line is $y = 1.476 - 0.0545x$.

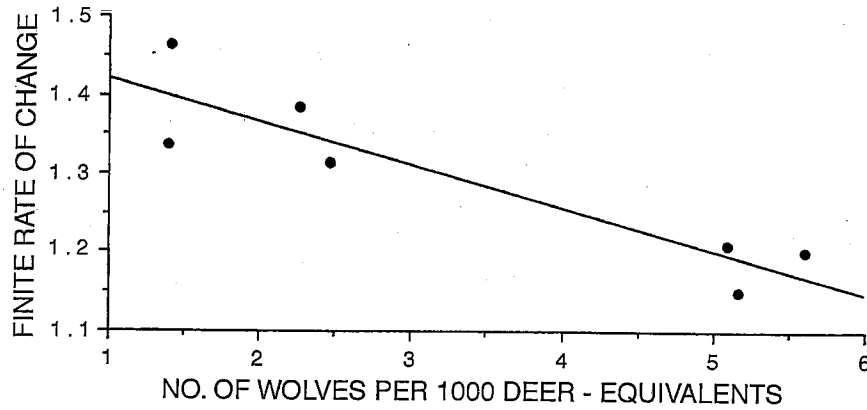
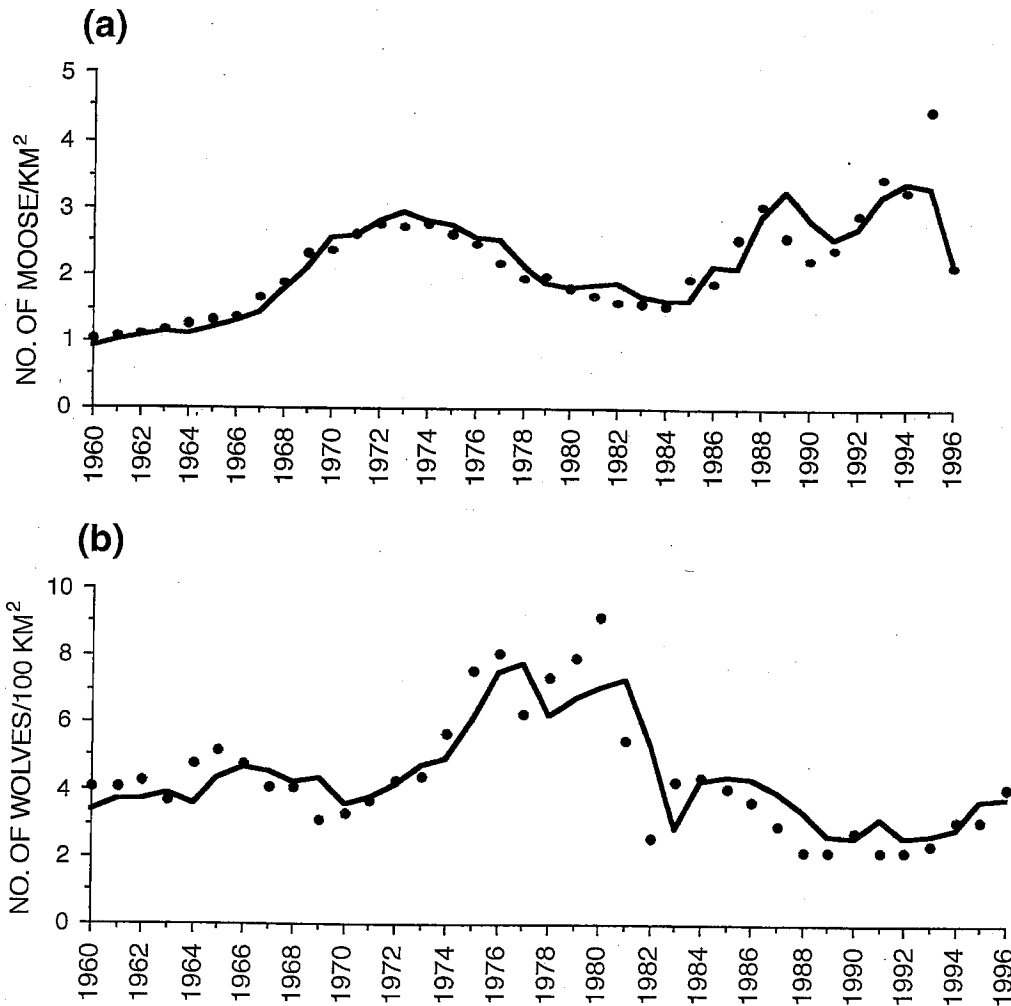


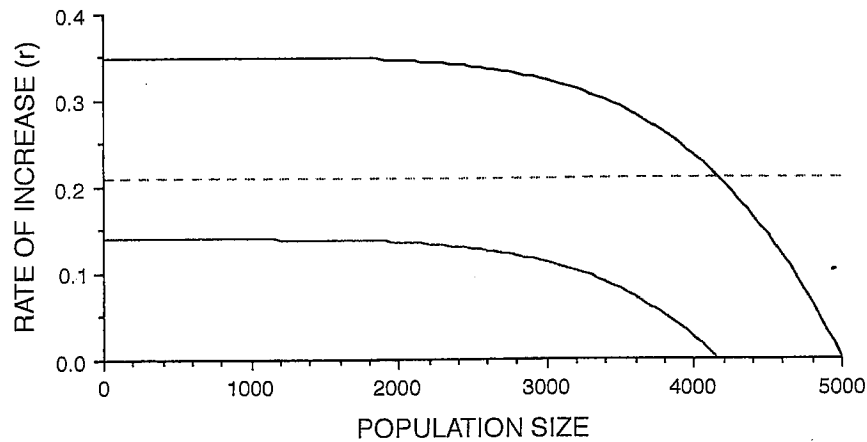
Fig. 2. Multiple-regression fits to moose (a) and wolf (b) data from Isle Royale supplied by Dr. R.O. Peterson (personal communication). Observed values are shown by the data points and model results by the line. See the text for further details.



alternative steady states. Hence, it is worthwhile to consider the behavior of eqs. 1 and 2 when plotted on the coordinate axes used by Messier (1994).

According to eq. 1, a prey population should follow the generalized logistic. If a predator population remains at the equilibrium level given by eq. 3, i.e., if $H = aV$ throughout the

Fig. 3. The hypothetical rate of increase (eq. 5) of a moose population subject to predation (lower curve) and in the absence of predation (upper curve). The broken line shows the removal rate ($ca = 0.21$).



growth of the prey population, then eq. 1 can be rearranged to give the rate of growth of the prey population as

$$[5] \quad r_t = \frac{V_t}{V_{t-1}} - 1 = r_1 \left[1 - \left(\frac{V_{t-1}}{K} \right)^z \right] - ca$$

Using parameters discussed above, the growth of a moose population might then proceed as in Fig. 3. Parameters used to develop Fig. 3 ($r = 0.35$, $ca = 0.21$) are those developed by Eberhardt (1997).

The present model thus admits only two steady-state conditions: one in the absence of predation and a second, lower level under predation. Growth of the moose population (Fig. 3) follows the conceptual model of Messier (1994), but the removal rate due to predation (broken line in Fig. 3) is here assumed to be constant, as shown by Eberhardt (1997), giving only one steady-state condition under predation. Messier (1994, Fig. 1) assumed the predation rate to follow a concave downward curve, which he claimed would yield various steady states, depending on how often it intersected the presumed growth curve for moose.

Multiple-prey models

In many circumstances, more than one prey species is available to wolves, posing the problem of determining the relative proportions of prey taken. The simplest assumption would seem to be that prey are taken in proportion to the relative biomass available. To examine such a model, the kill rates have been adjusted according to relative biomass, with one moose equal to three caribou. Caribou produce only single young, so a maximum rate of increase, $\lambda = 1.28$, has been used. Eberhardt et al. (1996) examined data on an elk population under very good conditions and concluded that $\lambda = 1.28$ is a likely maximum for this species with very similar life-history characteristics. Higher rates of increase for caribou have been reported (Keith 1983), but it seems likely that such rates are due to short-term fluctuations or sampling variation, and could not be sustained. A maximum rate of increase for moose might be obtained by assuming a first-year survival rate of 0.95 and an annual survival rate of 0.99 for subsequent years, single births at age 2, and 40% twinning (Ballard et al. 1991, Table 3) for older moose. Truncating at age 25 to approximate the effect

of senescence and using the Lotka–Leslie model (cf. Eberhardt 1985) give a maximum of $\lambda = 1.38$ for moose. The maximum rate of increase for wolves was estimated from Keith's data (Fig. 1) as $\lambda = 1.48$.

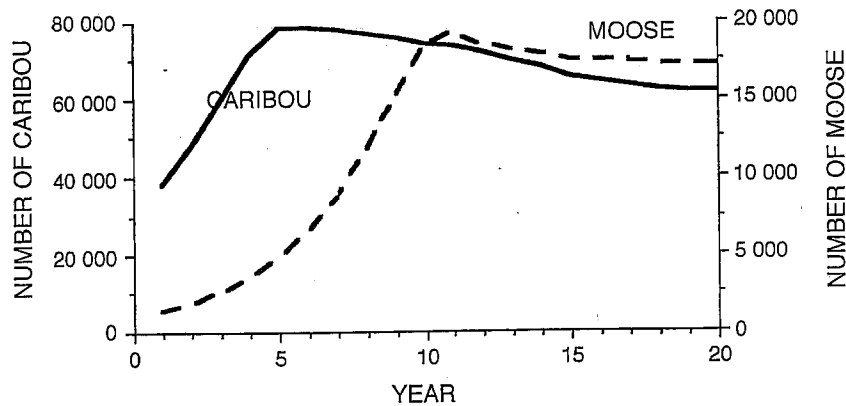
In trials, the rates developed above and an estimate of the equilibrium constant (a) as an average (209 deer-equivalents) of the pooled value from the data of Fuller (1989) and Messier (1994) and the value from the multiple-regression fit to Isle Royale data were used. Converting for moose gives $209/6 = 34.8$ moose per wolf each year, or $1/34.8 = 0.029$ wolves per moose. The data of Dale et al. (1994) averaged 0.086 caribou per wolf each day. Assuming 7 months of consumption of caribou per year yields 18 caribou per wolf per year. Eberhardt and Pitcher (1992) estimated 11.4 caribou per wolf each year in modeling wolf predation on caribou. About 7 moose per wolf each year is given above, which gives, on a biomass basis, $3(7) = 21$ caribou per wolf each year.

We thus use values of c for moose and caribou as a weighted average (weights of unity times the number of caribou, or 3 times the number of moose divided by the current biomass multiplied by the utilization rates for caribou (21) or moose (7)). The initial numbers were set at 30 000 for caribou ($K = 80\,000$), 1000 for moose ($K = 20\,000$), and 20 for wolves. The several populations achieved equilibrium (Fig. 4) within about 20 years, at about 17 000 moose, 62 000 caribou, and 1000 wolves.

Multiple predators

In the predator–prey systems considered here (ungulates and wolves in Alaska and Canada), there are two additional major sources of predation: bears and hunters. For most practical purposes, removals by hunting and trapping can simply be subtracted on the right side of eq. 1. However, selective harvests result in the need to treat males and females separately. Hunters may also select older animals, so an age-structured model dealing with the sexes separately may be required in the case of hunting harvests. Bear predation largely occurs shortly after calves are born (Adams et al. 1995). While it is evident that the extra energy thus provided to bears in the spring is important, bear numbers are not likely to be controlled by the availability of such prey. Hence, a working approximation can be obtained by adding another component of removal to eq. 1.

Fig. 4. Hypothetical trend of moose and caribou populations when kill rates are kept proportional to current biomass. Parameter values and further details are given in the text.



Discussion

I have tried to show here that simple versions of the Lotka-Volterra equations expressed as difference equations may serve to model actual data on predator-prey systems involving wolves and ungulates. The dependence of wolves on their ungulate prey base makes it seem certain that a complex and dynamic system needs to be considered, and it is difficult to see how one can hope to analyze such systems without considering prey and predator populations simultaneously. The model used here is very simple, but appears to provide at least a caricature of the actual system. Another trophic level should be considered if possible. McLaren and Peterson (1994) considered the relationship of the Isle Royale moose and wolf data to primary productivity.

As always, humans exert a strong influence on both predators and prey, so there are few prospects for studying the interaction without human influence. The Isle Royale situation is one exception, and the recent reintroduction of wolves into Yellowstone National Park may ultimately provide another example if adequate data can be obtained there. The Isle Royale data (Fig. 2) suggest oscillations in predator and prey numbers. Experience with eqs. 1 and 2 using the constants estimated here indicates that steady-state conditions are approached rather rapidly. Oscillations can be obtained by using more complex functional and numerical responses (May 1973, 1981). Alternative possible causes of the oscillations needing further study include the interaction between moose and vegetation along with the impact of variable snow depth on the moose population (cf. McRoberts et al. 1995).

More work needs to be done to determine whether the analyses suggested above can be truly useful, but it may be worthwhile to suggest a few prospects here. It had seemed to me that one of the most daunting prospects is the carrying out of any statistical analysis of predator-prey interactions, owing to the complexity of the interactions and the likely nonlinear nature of the models. It was thus something of a surprise that multiple-regression analyses were feasible, and it is to be hoped that this approach can be successfully pursued with additional data, and more attention given to statistical aspects. If nothing else is learned, we may expect to get a better idea of data needs. An example is provided by the controversy about the role of wolves in limiting moose numbers in Pukaskwa

Park (Thompson and Peterson 1988; Bergerud and Snider 1988). In their reply to criticism of earlier reports by Thompson and Peterson (1988), Bergerud and Snider (1988) present data on the numbers of moose and wolves for the years 1975 through 1979.

At first glance, one might hope that the multiple-regression model in eqs. 1 and 2 might be useful for examining these data. However, 5 paired observations supply only 4 pairs in the difference equations, which use observations at t and $t - 1$, and 4 pairs of observations provide no degrees of freedom for fitting eq. 2, inasmuch as 3 parameters must be estimated. As a rough rule of thumb, one needs 6-8 degrees of freedom to get any kind of stability in variance estimates, so it seems clear that we need at least 10-12 pairs of observations in order to consider trying the multiple-regression equations. Very likely, some Monte Carlo studies using the equations studied here would help us to decide when it may be practical to attempt the multiple-regression approach, and to be able to say something about the duration of studies needed. A number of studies in the literature report quantitative data on prey but only qualitative impressions of predator population trends. It may nonetheless be instructive to utilize the parameters arrived at above to see what the corresponding predator trend line might look like on the basis of prey numbers, and to compare this trend with the qualitative impressions reported in other papers. However, it seems clear that effective use of the predator-prey equations will require estimates of actual numbers of predators and prey. The difference equations used here are easily implemented in spreadsheets.

Another need indicated by the results given above is for a further look at data on predator-prey ratios. Theberge (1990) listed four confounding variables that may interfere with the use of prey-predator ratios to determine the impact of predation: (1) plasticity in the functional response of wolves to prey densities, (2) lags in the numerical response of wolf populations to changes in prey density, (3) the role of buffer prey species and the variable speed of prey switching, and (4) the proximity of the ungulate population to its nutrient/climate ceiling. In addition to these important factors, it is essential to know how the observed ratio developed. Estimates of the reciprocal of the critical ratio (a) in eq. 1 from two sources, the data of Fuller (1989) and Messier (1994) and the estimate given above from multiple regression on the Isle Royale data,

were in good agreement, but were double that obtained from Keith's (1983) data. This discrepancy requires more attention. Quite possibly, many of the data used by Fuller and Messier were obtained under non-equilibrium conditions, and there is thus a need to further examine the field data for indications as to whether an equilibrium was likely at the time they were collected.

Another aspect of the results above that needs more attention is the functional response. On the basis of the data reviewed by Eberhardt (1997), the functional response was reduced to a constant in the equations used here. This keeps the results reasonably simple, and there is a need for further investigation of this finding. Using a more complex functional response produces some of the theoretically more interesting oscillatory behavior in predator-prey dynamics but greatly reduces the prospect of estimating parameters from actual data. Huggard (1993) has presented data that suggest how functional response curves may arise from the ways in which predators encounter prey. Huggard (1993) also reports little evidence of prey selection when wolves used both deer and elk as prey, but Carbyn et al. (1993) reported in detail on wolf packs that appeared to specialize on bison (*Bison bison*). The multiple-prey model proposed here is thus largely speculative.

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