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STUDY TITLE: Development and Testing of a General Predator-Prey Computer Model for Use in Making Management Decisions

AUTHORS: Mark E McNay and Robert A DeLong

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SUMMARY

We completed development of a general predator-prey computer model named PredPrey. PredPrey runs in Microsoft®Excel version 5 or 7, under Windows®95. Microsoft® Visual Basic for Applications® programming was used to create a user interface that simplifies model inputs and allows the user to progressively increase the complexity of simulations. Model variables are entered by the user through dialog boxes that use standard Windows®95 controls. The user enters from 14 to 78 variables associated with predator-prey systems and environmental conditions, depending on the desired complexity of the simulation. PredPrey is designed as a self-tutorial program with an on-line user's manual accessible from any submenu, chart or table within the model.

The model is designed as a tool for use in making decisions for the management of big game, predator-prey systems. The model allows managers to explore short-term consequences of their management actions in the context of variable biotic and abiotic conditions. Functions are included which simulate the effects of: 1) harvest of predators and prey, 2) density dependence, 3) variable weather, 4) differences in prey vulnerability, 5) variation in predator functional and numerical responses to changing prey densities, 6) alternate prey, 7) changes in natural mortality rates of prey, and 8) variations in prey productivity.

PredPrey is a discrete-time model which simultaneously tracks changes in a single prey population (the Current Prey) in 2 annual cycles. The Biological Year cycle tracks population performance through simulated years 1 May–30 April, and the Harvest Year cycle tracks prey population performance through simulated years 1 November–30 October. Wolf populations are also modeled through Harvest Year and Biological Year cycles. Each model run simulates 20 years. The model accommodates simulated predation on the Current Prey by up to 3 predators of adult ungulates and 5 predators of neonate ungulates, simultaneously. Stochastic

functions for weather and wolf numerical responses can be enabled or disabled by the user. When stochastic functions are enabled, from 1 to 256 iterations of a single simulation can be chosen by the user. PredPrey allows the user to store and recall all the variables associated with a given simulation in a unique file with a user assigned name.

Mathematical equations which define model functions were taken from published predator-prey studies, derived from the analysis of empirical data, or created based on our understanding of theoretical relationships. We discuss our review of literature relevant to predator-prey interactions in northern North America ecosystems. The model prototype was tested by attempting to reproduce moose and wolf population changes that occurred in an Alaskan predator-prey system between 1965 and 1992 (Gasaway et al. 1983; Boertje et al. 1996). The test simulation closely tracked the empirical population responses of both wolves and moose to harvest, variable weather, a wolf control program, and density dependence. We consider the test results a first step in validating the model. Further testing using a variety of predator-prey empirical data sets and sensitivity testing is required.

Key words: computer model, density dependent, functional response, harvest, numerical response, predator-prey, prey vulnerability, stochastic weather, ungulate, wolf control, wolves.

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BACKGROUND

In 1991 a wolf (*Canis lupus*) management planning process stimulated increased public involvement in management of Alaska's big game species. Public requests to intensively manage for sustained high harvests of moose (*Alces alces*), caribou (*Rangifer tarandus*), and Dall sheep (*Ovis dalli*) from manipulated predator-prey systems were countered by public requests for lower, natural yields of big game from unmanipulated predator-prey systems. Those conflicting public values placed additional responsibilities on managers to more clearly predict consequences of proposed management programs. At the time, managers had few predictive tools. Arguments over the potential effects of specific management options often centered on arguments about the effectiveness of past management practices.

In response to similar controversies regarding predator-prey management, biologists in Alaska, other northern states, and Canada completed significant predator-prey research in the 1980s and early 1990s. Those advances in our understanding of predator-prey systems, advances in computer technology, and the common availability and use of personal computers were occurring simultaneously. Therefore we saw both a clear need and opportunity to develop a general predator-prey computer model to help managers make management decisions. We began work on the model called PredPrey in 1992.

THE USE OF MODELS

Starfield and Bleloch (1991) defined models and their use as "... any representation or abstraction of a system or process. We build models to 1) define our problems, 2) organize our thoughts, 3) understand our data, 4) communicate and test that understanding, and 5) make predictions."

In concept, building a predictive model for an Alaskan game population is simple. Changes in population size result from imbalances between factors that cause the population to increase (birth and immigration) and factors that cause the population to decrease (death and emigration). In practice, measurement of those factors may be difficult or impossible; therefore, models are always simplifications of reality. Starfield and Bleloch (1991) assert that "the quality of a model does not depend on how realistic it is, but on how well it performs in relation to the purpose for which it is built."

Our inability to precisely measure some variables (e.g., natural mortality rates) is not reason enough to exclude those variables from the model. "The initial structure of a model must be determined by the objectives, not by the available data" (Starfield and Bleloch 1991). Real world biological systems are infinitely complex, but the construction of a model is always confined by space, funding, personnel, and information. Good models strike a compromise that simulates the functional essence of the modeled system. Poor models can be overly complex, ambiguous, or so simplistic that significant functions of the system are ignored or misrepresented.

For the manager, models can be categorized as either conceptual models or management models. Conceptual models such as low-density dynamic equilibrium (Gasaway et al. 1992) and multi-density equilibria models (Haber 1977) describe the long-term dynamics of systems

but tell the manager little about the allowable harvest in the coming year. Conversely, management models such as those for estimating allowable yields of prey populations (Fuller 1989), or for estimating finite wolf population growth rates from an ungulate biomass index (Keith 1983), can be used by managers to explore short-term consequences of management actions or short-term biological responses in unmanipulated systems.

Management models that address population changes in a single species are termed single-species models. Such models may incorporate the effects of predation, habitat, and weather, but they often do not explicitly model feedback interactions within the ecosystem. Consequently, single-species models are limited in their ability to predict the effects of manipulating populations of some species to benefit populations of other species. A system or community model is required to model the effect of one species on another and/or the effects of abiotic factors (i.e., environment) on the biotic parts of the ecosystem. System models are inherently more complex than single-species models and during development can easily become unwieldy and overly complex. To prevent this, the model builder must start with a clear set of objectives and confine the model functions to meet those objectives.

There are abundant examples of models used to describe predator-prey-human interactions in northern ecosystems (Keith 1983; Van Ballenberghe and Dart 1983; Ballard et al. 1986; Bergerud and Elliot 1986; Ballard et al. 1987; Fuller 1989; Hayes et al. 1991; Schwartz and Franzmann 1991; Gasaway et al. 1992). Each is based on empirical evidence of basic relationships between components of the predator-prey system. As more studies are completed, many of those basic relationships seem to be consistent and, therefore, somewhat predictable. Models built to describe those relationships often relate to only a portion of the system, e.g., maximum sustained yield of moose (Van Ballenberghe and Dart 1983) or number of moose calves consumed by black bears (*Ursus americanus*; Schwartz and Franzmann 1991). None is available to Alaskan managers in the form of easily used computer models that simultaneously combine the potential effects of weather, predation, harvest, density dependence, prey vulnerability, productivity, and population composition on ungulate population dynamics.

AVAILABILITY OF REQUIRED INFORMATION

Model construction requires estimates of production and survival of young, estimates of mortality rates, differences between immigration and emigration, harvest levels, and estimates of population size and composition. In Alaska, production and survival of young among caribou, moose, and sheep are estimated annually through routine survey-and-inventory programs and are reported in annual management reports (e.g., Morgan 1990). Estimates are expressed as young:100 females or as percent young in the population. Estimates of the number of juvenile recruits are derived by combining those composition ratios with total population estimates. Total population estimates are based on stratified random sampling for moose (Gasaway et al. 1986), aerial photography for caribou (Davis et al. 1979), or total counts in key areas for sheep (Heimer and Watson 1986; Whitten and Eagan 1995) and bison (*Bison bison*) (Carbyn et al. 1993). Deer (*Odocoileus* spp.) population estimates in heavily forested areas are based on pellet group transects (Kirchhoff 1990).

Causes of mortality are generally considered in 3 categories: 1) harvest by hunters, 2) predator-caused mortality, and 3) other nonpredator natural mortality. Harvest is determined annually from mandatory hunter reports and in some cases substantiated with checkstations (McNay 1992). Nonpredator-caused natural mortality is often related to severe weather (Coady 1974; Gasaway et al. 1983), and qualitative estimates can be based on winter severity indices. Site-specific intensive monitoring of moose and caribou populations provide quantitative estimates of nonpredator natural mortality that may be generally applicable to other areas with similar weather and habitat conditions (Bangs et al. 1989; Ballard et al. 1991; Davis et al. 1991; Modafferi and Becker 1997).

Predation is a large component of natural mortality in most northern ecosystems. Estimates of predation rates require intensive radiotelemetry studies which are rarely part of routine survey and inventory programs, but several intensive studies completed in the United States and Canada provide a sufficient range of values to model potential effects of predation. Grizzly bears have repeatedly been shown to be important predators of both adult and juvenile ungulates (Boertje et al. 1988; Larsen et al. 1989; Ballard et al. 1990). Black bears are important predators of neonate ungulates (Adams et al. 1989; Osborne et al. 1991; Schwartz and Franzmann 1991). As obligate carnivores, wolves prey upon ungulates at more consistent rates than do bears. Using data from other Alaskan (Peterson et al. 1984), Canadian (Fuller and Keith 1980), and their own studies, Ballard et al. (1987) described a relationship between pack size and kill rates which recognized that a reduction in average pack size results in a proportionately smaller reduction in wolf predation rates (Hayes et al. 1991). Fuller (1989) used results from 25 North American studies to propose a general relationship describing a theoretical carrying capacity for wolves, and Keith (1983) described a general relationship from 7 North American studies between the ungulate biomass index and the finite growth rate of wolf populations.

Those and other relationships can be combined to model wolf and bear predation rates, wolf population response to changing ungulate densities, and, conversely, ungulate population responses to changing wolf and bear densities. Responses of ungulate populations to extreme weather can be modeled using: 1) data describing thresholds of critical weather such as described for moose by Coady (1974) or 2) studies that provide empirical effects of certain weather events on specific ungulate populations (Bishop and Rausch 1974; Boertje et al. 1996; Modafferi and Becker 1997). Historical weather records from a given locality can be used to simulate the probability of a severe weather event.

Without radiotelemetry data, population estimates of large seclusive predators such as bears and wolves have customarily been subject to skepticism. However, recent advances in census techniques for bears (Miller et al. 1997) and wolves (Ballard et al. 1995; Becker et al., in press) now provide opportunities for improved estimates of bear and wolf population size.

GOAL

To develop an easily used computer model to assist wildlife managers in making annual management decisions regarding big game predator-prey systems and to enhance biologists' understanding of predator prey systems.

OBJECTIVES

- Conduct a literature review of predator-prey studies to identify basic relationships of Alaskan predator-prey systems.
- Construct a general predator-prey model using Microsoft®Excel for Windows®95 software.
- Write a manual describing model function and basis for model assumptions, including guidelines for model use. The user's manual will be included in the model as a Help file.
- Compile and analyze predator-prey data for western Unit 20B for the period 1984–1989. Prepare a report describing predator-prey dynamics in western Unit 20B.
- Validate and refine model functions to simulate known dynamics of intensively studied predator-prey systems.
- Train area biologists in use of the model and application to current management problems.
- Write final report and prepare presentations for public and scientific meetings.

METHODS

SYSTEM REQUIREMENTS AND USER INTERFACE

The original model prototype written in Lotus®1-2-3 for DOS® was converted to Microsoft®Excel for Windows®95. Submodels were arranged on individual Microsoft®Excel worksheets. A user interface programmed in Visual Basic® allows the user to move within the model with push buttons, rather than scrolling and typing. Model variables are entered by the user through dialog boxes using standard Microsoft® for Windows®95 controls. Cells of worksheets are protected from direct editing, and changes in variables are made only through dialog boxes; this approach simplifies data entry, prevents inadvertent parameter changes, and allows a point and click type of data manipulation that simplifies use, increases speed, and enhances interpretation of results.

Our goal is to provide a model that is sufficiently general to apply to a variety of large ungulate predator-prey systems. However, that requires inputs to customize model parameters for a variety of biological communities influenced by environmental variables. As user options are created, model complexity increases.

We envisioned some users being interested only in the effects of harvest in a single-species system, ignoring more complex effects such as stochastic weather, differential prey vulnerability, multiple predators, alternate prey, and variable production. Other users will want to progress from simple to more complex simulations. To allow maximum flexibility of use while maintaining ease of operation, we compartmentalized user dialog boxes. With this design the user can progress from simple to complex simulations and stop at the desired level of complexity.

We expect most users will work with a given management or research simulation during several work sessions. Rather than requiring the user to reenter the desired input values during each work session, PredPrey allows the user to store all the input values associated with a given simulation in a unique file with a user assigned name. One such set of values is termed a model state. Individual model states are saved and recalled using standard Windows®95 dialogs that are accessed by push buttons in the main menu.

Initially, PredPrey is loaded with a default model state that simulates a harvested moose-wolf predator prey system at equilibrium in the absence of weather effects. Default model states can be created, changed, deleted or recalled by push buttons in the Default Model State dialog box. This feature is particularly useful for users who rarely create complex simulations. By entering the default state and then making desired changes only in the Basic Inputs dialog box, the user is assured that errors in entry for more complex variables will not affect the simulation.

PredPrey is designed as a self-tutorial program. The entire text of the user's manual is available through a help menu accessible from any dialog box, chart, or table within the model. When operating within any dialog box, users may select help to retrieve information explaining functions controlled by that particular dialog box, chart, or table. In the main menu choosing Help retrieves an outline of the entire user's manual. From that outline the user clicks on the appropriate section to retrieve the desired information. This process is identical to standard Windows® help functions.

A number of reference tables and charts in the online Help menu provide samples of empirical values corresponding to model input variables. The empirical data were extracted from published studies of North American predator-prey systems. Users can access this reference table to bracket input values if they do not have empirical data from their managed population.

MODEL FUNCTIONS AND CHARACTERISTICS

Mathematical equations that define model functions were often taken directly or modified from published predator-prey studies. In other cases equations necessary to define model functions were not available in the published literature, or contradictory relationships were described in different reports. When necessary we created equations to define model functions based on conceptual rather than quantitative results, and when contradictory relationships were reported, we selected a function based on our view of its general applicability. We also tested equations by simulation and evaluated the results in terms of their conceptual fit to published theories.

PredPrey is a discrete-time model. The user has the option of selecting deterministic or stochastic weather parameters. Weather severity affects mortality of all sex and age classes. With the deterministic function, the user has 2 options: 1) no adverse weather effects or 2) adverse weather events for selected years. When stochastic weather is selected, adverse weather occurs based on user-specified probabilities.

The model simulates changes in population size, composition, allowable harvest, mortality, and productivity of 1 ungulate population called the Current Prey. Populations of up to 7

alternate prey may also be entered. PredPrey does not simulate dynamics of alternate prey, but alternate prey numbers are used in the calculation of total ungulate biomass. Changes in total ungulate biomass affect wolf population growth rates, which in turn may affect the Current Prey Population.

Both predator and prey populations move through an annual cycle with discrete time points in the cycle where populations are adjusted for mortality and production. For the prey population, 2 annual cycles (harvest year cycle and the biological year cycle) are calculated simultaneously in different submodels. The harvest year cycle runs in the Primary Population submodel and begins on 1 November of the entry year. Overwinter predator- and nonpredator-caused mortality of the Current Prey population are subtracted from the 1 November population before production of neonates. Juvenile, yearling, and 2-year-old cohorts advance in age before production. Production occurs at the beginning of the biological year cycle (1 May) and is based on the number of females in the reproductively eligible cohorts. Autumn harvest and summer natural mortality are subtracted simultaneously at the end of the harvest cycle year (31 Oct) to yield the starting population on 1 November for the next year. The model does not contain a senescence function for either mortality or production; all population members older than 3 years of age are considered adult. The biological year calculations facilitate estimates of mortality distribution among all sex and age classes from the peak annual population that results from calf/fawn production.

MODEL TESTING

To test PredPrey's ability to simulate real world Predator-Prey systems, we created a simulation of moose and wolf populations for an Interior Alaskan predator-prey system. We used the documented case history of Unit 20A for the period 1965–1992 as the empirical data set (Gasaway et al. 1983; Boertje et al. 1996). The Unit 20A case history is complex, involving: 1) a dramatic population decline followed by an increase in the moose population, 2) a wolf control program, 3) periodic severe weather events, 4) variable natural mortality rates resulting from periodic severe weather and age structure shifts in the prey population, 5) an initial decline, believed to be related to density dependence, 6) major shifts in the population age structure of moose, 7) multiple harvest strategies including males only and either sex harvest of moose, 8) variable harvest rates of wolves by private trappers, and 9) distribution of alternate prey (caribou and Dall sheep) in roughly ½ of the study area, but distribution of moose and wolves throughout the study area.

PredPrey is designed for short-term simulations (maximum time span = 20 yr) and cannot accommodate the entire 27-year history in a single simulation. We divided the case history into 2 simulations, one for the period of decline (1965–1974) and a second for the period of moose population increase (1975–1992). The decline simulation was initialized using the empirical data set (Gasaway et al. 1983). The recovery simulation was initialized using moose and wolf population data from the decline simulation.

We incorporated density dependence as a factor in the initial decline (Bishop and Rausch 1974) but assumed that after 1967 density dependence did not affect the decline in the moose population (Gasaway et al. 1983). We used a mean pregnancy rate of 89% for both

simulations (Gasaway et al. 1983) but a higher twinning rate (25% vs 15%) during the recovery period to reflect the higher twinning rates reported by Gasaway et al. (1983) for the early years of moose recovery.

Baseline nonpredator natural mortality rates of adult females, adult males, first winter calves, and neonates were set at 4%, 6%, 10% and 25%, respectively. Those rates were adjusted for each year by the application of deterministic weather severity indices estimated from the qualitative descriptions in the case history documentation (Bishop and Rausch 1974; Gasaway et al. 1983; Boertje et al. 1996).

Harvest of moose was simulated by entering the published harvest rates for male and female moose from Gasaway et al. (1983) for years 1965–1978 and from Boertje et al. (1996) for later years. Wolf control prescriptions were entered as mean values of autumn wolf populations during years of control and as mean values for public harvest of wolves during years when wolves were not controlled. A simulation of entire pack removal was entered for the 1975–1982 wolf control program.

The only data available regarding the composition of wolf diet came from a 1989 kill rate study when caribou were at an all-time population high of approximately 10,000 caribou. At that time, moose comprised approximately 81% of the biomass in the diet of 4 monitored wolf packs within Unit 20A (McNay 1990). That value was used as the winter predator load for recovery period simulation when caribou and moose numbers were roughly equal, but a higher value of 0.9 was assigned as the predator load for the declining period 1965–1975, when moose populations were generally much higher than caribou. Summer predator loads were entered as 70% of winter values based on observed summer kill rates of moose in a moose-caribou-wolf system in Southcentral Alaska (Ballard et al. 1987).

Vulnerability of different sex and age classes of moose to wolf predation probably changed during the 30-year period, but there was no empirical measure of vulnerability. Moose calves during winter may be more vulnerable to wolf predation than adults (Peterson et al. 1984), but during adverse weather or when moose are in marginal physical condition adults may be equally vulnerable (Ballard et al. 1997). We define the index to vulnerability as the proportion of a particular sex and age class among the total moose killed by wolves divided by the proportion of that sex and age class found in the moose population. We assumed equal vulnerability across all sex and age classes during the period of moose population decline (Vulnerability index = 1.0) and assumed adult moose had lower vulnerability (Vulnerability index = 0.40) to wolf predation during the early recovery period when weather was mild and the age structure of the moose population was young to middle aged. We assumed yearlings and calves were more vulnerable to wolf predation than adults during the recovery period (Vulnerability index = 3.0 and 4.0, respectively).

Grizzly bears are throughout Unit 20A, but their densities are highest in the foothills of the Alaska Range. Grizzly densities are much lower on the lowlands where moose calving occurs and where moose are concentrated during summer. We extrapolated a total estimate of 260 grizzly bears for the study area, based on density estimates from the foothills and mountains (Reynolds 1997), but used a simulation of 100 bears to reflect the lower density around moose

summer concentrations. We used the deterministic Wolf Population Growth Function for both simulations (Appendix A).

For initiation, the model requires estimates of the proportion of neonates killed by wolves, bears, and other predators. Those initial proportions, however, only apply to the first year of the simulation run. The proportions change in subsequent simulated years as predator and prey numbers change. In the decline simulation, we used initial proportions of 6%, 11%, and 15% for the proportion of neonates taken by grizzlies, black bears, and wolves, respectively. For the recovery simulation we began with those proportions, then adjusted them until the resulting calf:cow ratios mimicked those of the empirical ratios. Those adjustments resulted in initial proportions of 8%, 15%, and 12% for the proportion of initial year neonates succumbing to grizzly, black bear, and wolf predation, respectively.

After the test simulations were completed, we reinitialized both the decline and recovery simulations with the original population inputs, then enabled stochastic weather and stochastic wolf population growth. We ran 10 iterations of each stochastic data set and compared the multiple iterations of the total moose population response with the deterministic test simulations.

RESULTS AND DISCUSSION

SYSTEM REQUIREMENTS AND USER INTERFACE

PredPrey has the following system requirements:

Processor:	Pentium 60mhz (minimum) 90mhz or greater (recommended)
Video:	Color VGA (minimum)
Hard drive:	10MB free space
Memory:	16MB RAM (minimum)
Operating software:	Windows®95 or WindowsNT™ with Microsoft®Excel 5 or 7

Seven submodels contain calculations related to submodel categories (Table 1). PredPrey extracts calculated values from the various submodels for display in user-interface charts and tables, but the user may also access the individual submodel worksheets. The current version of PredPrey contains 390 lines of calculations in the combined submodels. Most of those produce intermediate values used to calculate population parameters displayed by the user interface; however, many of those values are also of interest by themselves. For example, as we simulate a moose population, the proportion of autumn calves to total cows is depicted in the Sex and Age ratio chart, but managers may be more interested in the proportion of calves to cows >30 months of age. That ratio is calculated on line 21 in the Primary Population model and can be referenced only by entering that submodel worksheet and reading the simulated values directly from the line of calculations. A complete list of submodel calculation titles and initial year formulas is given in Appendix B.

The user operates the model from the Main Menu which provides push button controls to access Basic and Advanced Input dialog boxes, 2 table outputs, 18 chart outputs, 7 submodel

worksheets, the online help menu, and controls to load and save completed model simulations (Appendix C). Data entry begins in the Basic Inputs dialog. Spinners, checkboxes, radio buttons, or push button controls are provided for input of 14 potential Current Prey variables, 21 potential variables associated with up to 3 simultaneous predators on adult ungulates, 5 variables associated with predation on neonates by up to 5 simultaneous predators, 5 harvest variables, 4 potential variables for alternate prey, and up to 9 environmental variables. The user does not have to enter each variable for each run but may recall a saved model state from a previous work session. The number of entries required for a given simulation increases as the complexity of the simulated system increases. Simulations that do not involve predators or alternate prey may require as few as 14 total entries, but users have the option to manipulate up to 78 variables accessed from the Basic and Advance Input dialogs.

The Advanced Inputs dialog box provides opportunity to increase the complexity of model simulations by introducing prey vulnerability to predation, functional responses by predators to changes in prey density, and stochastic functions. Stochastic weather and stochastic wolf growth result in variable performance of prey populations to a single set of inputs. Up to 256 iterations may be selected for a given stochastic model run, and the output is graphed on a single Current Prey population chart.

MODEL FUNCTIONS AND CHARACTERISTICS

Nonpredator Natural Mortality of Ungulate Prey

In natural systems, mortality within ungulate populations varies widely dependent upon predator densities, environmental effects, and habitat conditions. Among studies reporting high rates of natural mortality, weather is often the most significant single factor associated with natural mortality rates. Bishop and Rausch (1974) estimate up to 50% of an Interior Alaska moose population died during a single deep snow winter. Similarly, 71% of the bull moose and 35% of the cow moose died during a deep snow winter in Southcentral Alaska (Modafferi and Becker 1997), and an estimated 22% of the adult cows in the Delta Caribou Herd died during a single winter (Valkenburg 1997). However, in a separate Southcentral Alaskan study area, mortality on adult cow moose was estimated at only 8% during a deep snow winter (Ballard et al. 1991), a rate only slightly higher than estimated for moderate winters.

In the absence of severe weather, nonpredation natural mortality rates for adult moose and caribou are often low (Table 2). In modeling natural mortality of Prey species, PredPrey requires inputs of nonpredator natural mortality rates for 4 sex/age classes of Current Prey, neonates (0–6 months), juveniles (6–18 months), adult females, and adult males. When weather effects are disabled, the entered rates apply to mortality calculations in all simulated years. When weather effects are enabled (either Deterministic or Stochastic), the entered rates are multiplied by weather severity factors that reflect the simulated weather severity of a particular year. Weather severity factors in Stochastic Weather simulations range from 0.5 to 5.0; therefore, nonpredator mortality rates could potentially increase 5-fold during severe weather years.

To prevent unrealistically high rates of natural mortality, PredPrey includes a Maximum Annual Mortality (MAM) Function that limits nonpredator natural mortality within model simulations. The MAM value varies with the Current Prey population to estimated Carrying Capacity ratio. At Carrying Capacity, the MAM value reaches 50%, then declines to a maximum of 25% at and below a Current Population to Carrying Capacity ratio of about 0.2 (Fig 1). The MAM function is disabled when the Deterministic Weather or No Weather options are selected; therefore, users are cautioned to use the Survival Rate Chart as a model check to ensure the combination of initial entries and deterministic weather severity factors do not result in excessive rates of total natural mortality.

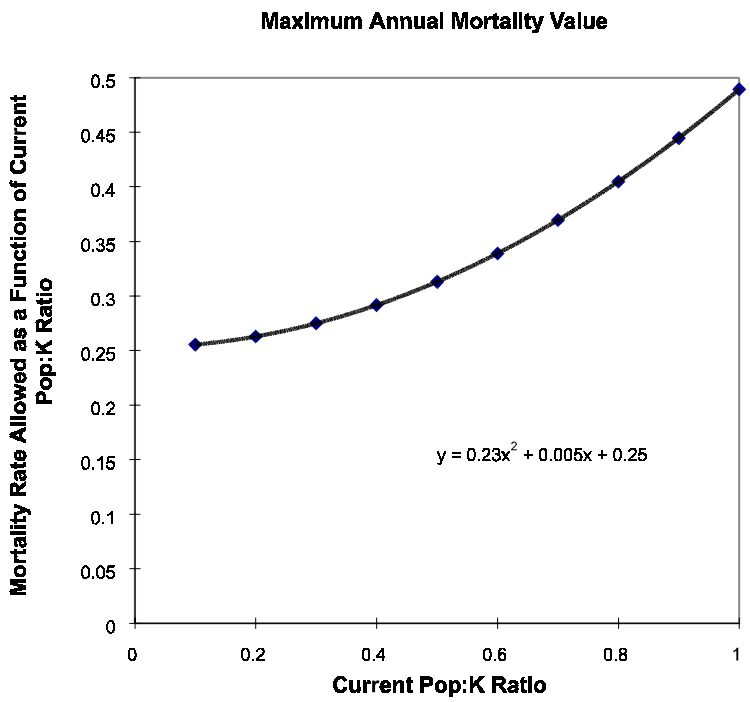

Figure 1 The Maximum Annual Mortality Function, which controls the amount of nonpredator mortality among the Current Prey within PredPrey

To calculate total nonpredator natural mortality for the Current Prey population, PredPrey compares the MAM value with the sum of all predicted natural mortality sources (i.e., predation and nonpredation). If the summed natural mortality exceeds the MAM value, then the nonpredator natural mortality is reduced or eliminated. Therefore, nonpredation natural mortality rates may be low even during severe weather if predation rates are high or if the Current Prey population to Carrying Capacity ratio is low.

Wolf Predation Function

Simulated predation by wolves on the Current Prey is controlled by a predation function, $Y = 13.84-3.22\ln(x)$, where y = the number of days between the kill of 1 adult moose equivalent by a wolf pack, and x = individual wolf pack size. The function was derived from observations of individual wolf packs and their kill rates among 3 wolf-prey studies in Alaska and Alberta (Ballard et al. 1987). This predation function results in a decreasing per wolf kill rate as wolf

pack size increases (Fig 2). Similar relationships between wolf pack size and per wolf kill rate were described for other wolf-prey systems in Northwest Alaska (Ballard et al. 1997) and Yukon (Hayes 1995).

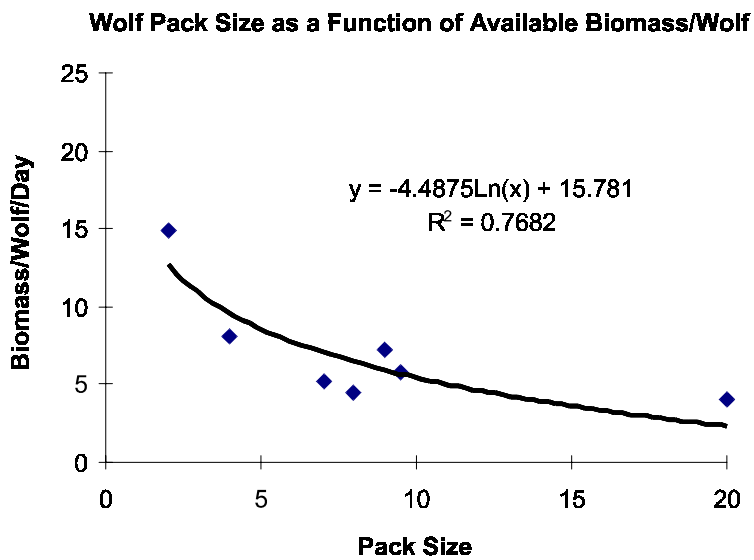

Figure 2 Relationship between wolf pack size and the availability of edible biomass/wolf/day resulting from PredPrey Predation Function (calculated from Ballard et al. 1987)

Using Ballard et al.'s (1987) function to model wolf predation requires a kill rate be calculated for each individual wolf pack. The sum of those kill rates yields the estimate of Current Prey biomass killed by the wolf population (see Equation 1 below). Therefore a simulation involving a wolf population of 20 packs would require 20 calculations. Alternatively, the total kill rate can be calculated by a single equation if mean pack size is substituted for individual pack size (see Equation 2 below), but that ignores the variability in kill rates associated with the potential wide range of pack sizes present in real wolf populations.

We evaluated a predation function based on mean pack size versus a function based on calculation of individual pack kill rates by constructing a simulation model. We ran 1000 simulations of wolf kill rates. The simulations produced kill rates from populations that randomly varied from 1 to 50 packs with pack sizes randomly ranging from 2 to 25 wolves. A "true kill" was calculated for each of the 1000 simulated populations as the sum of individual pack kills for each simulated population. For each simulation, the "true kill" (Equation 1) was compared with the kill produced by a) Ballard's function modified by substituting the mean pack size for individual pack size (Equation 2) and b) a Taylor Expansion Series of Equation 2 which estimated the variance resulting from different individual pack sizes (Equation 3; J Ver Hoef, pers commun). The results were evaluated based upon the distribution of the percent difference from the "true kill" resulting from Equations 2 and 3. The modified function without correction for variance (Equation 2) slightly underestimated the true kill value (mean percent error = -0.39%) and the Taylor Expansion Series Function (Equation 3) slightly overestimated the true kill ($\bar{x}$ % error = 0.26%), but the Taylor Series

corrected function had a higher variance and occasionally exhibited a large deviation from the true kill (Fig 3).

The equations used in the simulation were as follows (where Y = the adjusted days per wolf kill of 1 moose adult equivalent, x = size of individual packs within the population, and $\bar{x}$ is the population mean pack size):

Equation 1: $Y_1(x_1, x_2 \ldots x_n) = \sum_{i=1}^{n}(13.84 - 3.22 ln(x_i));$

Equation 2: $Y_2(\bar{x}) = n[13.84 - 3.22 ln(\bar{x})];$

Equation 3: $Y_3(\bar{x}) = \sum_{i=1}^{n}\left[\frac{Y_2(\bar{x})}{n} + (x_i - \bar{x})\frac{y'(\bar{x})}{n} + \frac{(x_i - \bar{x})^2}{2}\frac{y''(\bar{x})}{n}\right];$

We selected the Ballard et al. (1987) modified function as the Predation Function (i.e., substituting mean pack size for individual wolf pack size) without the Taylor expansion correction for variance. This greatly simplified calculation of wolf kill rates and closely approximated Ballard and others' (1987) theoretical function. The Predation Function results in an estimate of the total kill of Current Prey by wolves expressed in adult moose equivalents of biomass. An estimate of per wolf consumption rates was then produced by converting the total kill to biomass (kg) and dividing by the number of wolves.

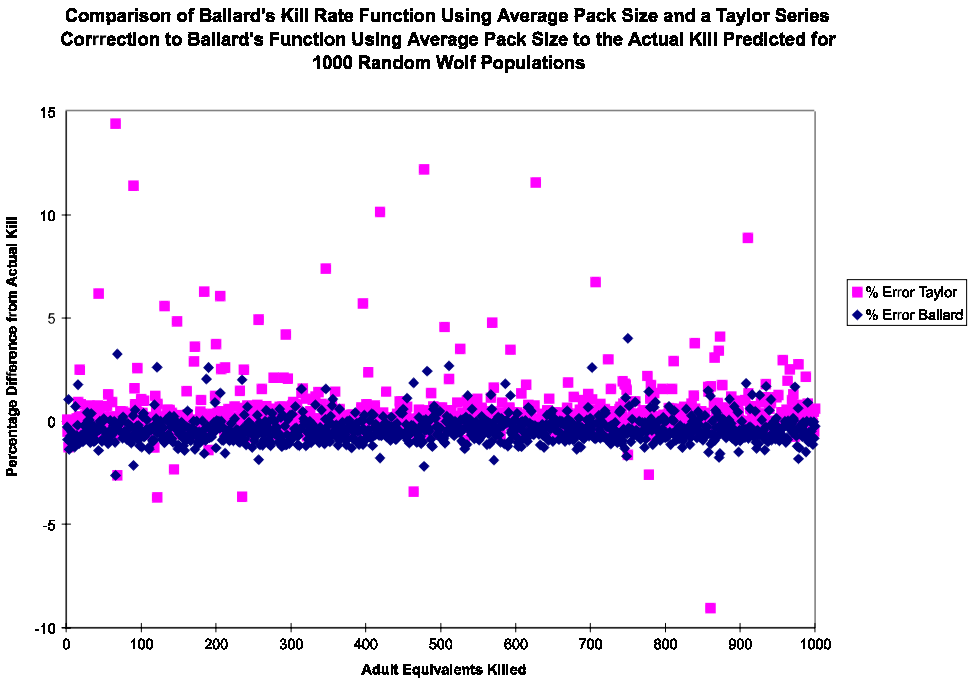

Figure 3 Results from 1000 randomly generated wolf populations and the kill rates generated by Equations 2 and 3. Dark diamonds represent kill rates generated without correction for pack size variability (Equation 2), and light squares represent kill rates generated by applying a Taylor Series expansion to the modified equation to correct for pack size variability (Equation 3).

Consumption rates within a given wolf population may vary seasonally (Peterson et al. 1984), and exhibit a wide range of values between populations and prey types (Table 3). Fuller (1989) reviewed 14 North American studies and found daily wolf consumption rates ranged from 2.0 to 7.2 kg/wolf. Where small ungulates were the primary prey (deer and sheep), consumption rates were lowest, ranging from 2.0 to 3.0 kg/wolf/day. Consumption rates were 4.5 to 7.2 kg/wolf/day when large ungulates were the primary prey (moose, bison, and elk [*Cervus elaphus*]). Estimates of annual kill rates range from 15 to 33 deer/wolf/year (Table 4), and from 1.9 to 15 animals/wolf/winter among a variety of larger ungulate prey where winter wolf predation rates were measured (Table 5). To accommodate variability in consumption rates PredPrey allows the user to adjust both the seasonal and overall predation rate on simulated wolf populations to match empirical values.

There is some confusion in the literature regarding the use of the term “wolf consumption rates.” Most studies (Peterson 1977; Fuller and Keith 1980; Peterson et al. 1984; Messier and Crete 1985; Ballard et al. 1987) assume that most of the biomass killed by wolves is consumed but a proportion of the kill biomass is inedible. A consumption coefficient is often used to correct for inedible biomass, subtracting some proportional value to account for bones,

hide, rumen, etc. In at least one case, however, correction values for scavenger consumption of prey was also used in calculating wolf consumption rates (Hayes et al. 1991). In that study raven scavenging of moose carcasses accounted for 10% of edible biomass from a pack of 10 wolves, 20% for a pack of 6, 50% for a pair, and 66% for lone wolves.

In PredPrey we use the term consumption rate to represent the amount of edible biomass available per wolf. We correct for inedible biomass, but do not correct for edible biomass consumed by scavengers. The total predicted biomass killed per wolf is calculated from total predicted kill, wolf population size, and weights of individual prey. PredPrey adjusts total per wolf biomass values for inedible portions of prey carcasses by multiplying per wolf biomass by consumption coefficients that can be changed by the user. Consumption rates reported in the Consumption Rate chart are given as kg/wolf/day, but are also calculated and listed in the PM submodel as kg biomass/kg wolf/day, assuming a weight of 40 kg per wolf.

Functional Response

Rarely, if ever, have predators caused the extirpation of their prey in large carnivore-ungulate, predator-prey systems. Possible exceptions are found: 1) on islands where immigration and emigration are restricted (Klein 1995); 2) where population declines, exacerbated by predation, cause changes in ungulate distribution and, consequently, the localized absence of ungulates (Valkenburg et al. 1994); or 3) where alternate prey sustained high predator densities and predators continued to prey on the less abundant, declining prey species (Seip 1992). More commonly, large declines in ungulate populations are followed by a low-density dynamic equilibrium (LDDE) where both ungulate and obligate predator populations exist at varying but generally low densities (Gasaway et al. 1992).

The conversion from a state of high ungulate abundance to a LDDE state occurs through numerical and functional responses of predator populations to changes in prey abundance. The conceptual basis for wolf-ungulate functional responses was summarized by Seip (1995) and Messier (1995). However, there are differences in the reported shape of the functional response curve (Messier 1994 vs. Hayes 1995), and one study failed to show a clear functional response except at extremely low prey densities, possibly because of rapid numerical responses or differences in the social behavior of prey (Dale et al. 1995).

The PredPrey Functional Response is incorporated into predation calculations for wolves, grizzly bears, and optional predators. With the goal of preventing prey population extirpation, and with the assumption that no single functional response equation can be applied to the possible variety of predator-prey systems, we developed the following Michaelis-Menten equation (Fryxell 1991; Messier 1994) to generate a Functional Response Coefficient (FRC): $Y = 1.32*(x-25)/(x-.01)$, where Y = Function Response Coefficient and x = the ratio of the Current Prey biomass to a Biomass Threshold. Kill rates calculated by the Predation Function are multiplied by the FRC to generate a functional response curve (Fig 4). By using the ratio of current:threshold biomass to generate a Functional Response Coefficient, PredPrey allows the user to change the shape of the functional response curve or eliminate it entirely (Fig 5).

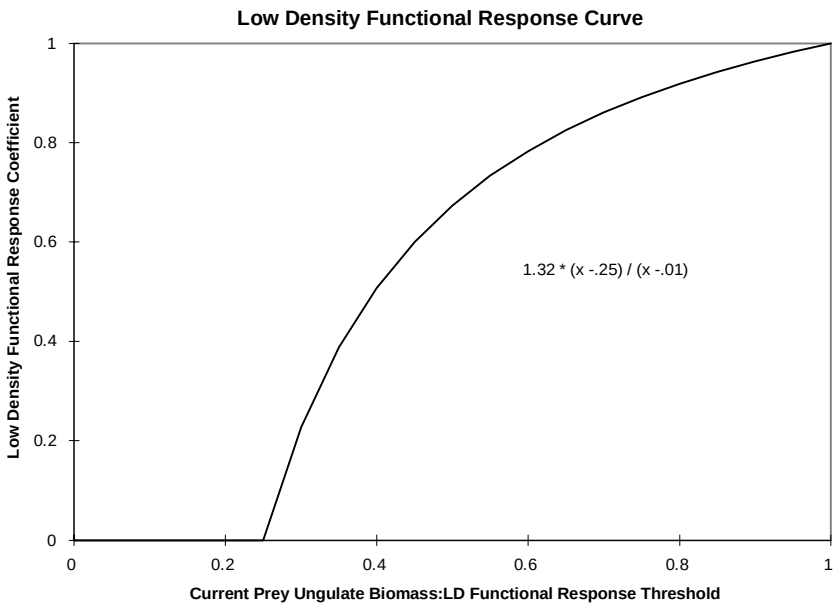

Figure 4 The modified Michaelis-Menten Function used to control the PredPrey Functional Response of predators to changes in prey populations.

The Functional Response is triggered when the total biomass of the autumn Current Prey population declines below a user-entered Biomass Threshold. The threshold is entered as kilograms of biomass per 1000 km^2. We used biomass rather than animal density as the threshold value because biomass reflects a more general condition and requires less manipulation of user entries. If animal density was used to trigger the functional response, a new threshold entry would be necessary for each prey type to adjust for the change in weight of each prey item. We provide a series of charts in the user's manual to assist users in selecting Biomass Thresholds (Appendix A).

When the Current Prey Biomass falls below the threshold value, kill rates of Current Prey by all predators decline. At values above the threshold, the functional response coefficient defaults to 1. Changes in the per wolf kill rate may occur above the Biomass Threshold, from changes in population mean pack size over time, but the PredPrey Functional Response itself has no effect when current prey biomass is above the threshold. If the user selects a Biomass Threshold value of zero, the Functional Response Coefficient defaults to 1, eliminating all functional responses by all predators from the simulation.

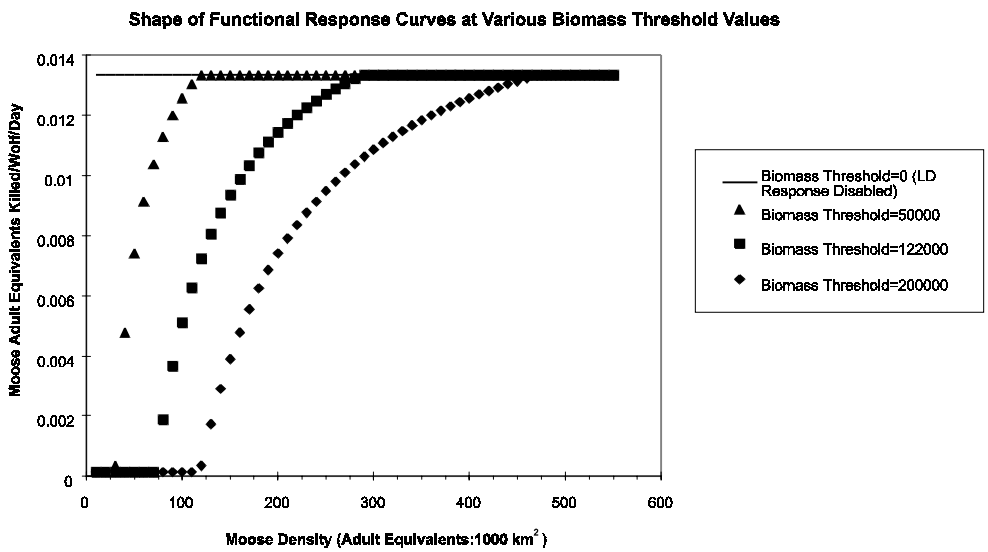

Figure 5 Examples of how the user can change the shape of the functional response curve by changing the Biomass Threshold Value

Numerical Responses

A positive correlation of wolf population growth rates and maximum wolf densities with ungulate prey biomass has been the conceptual basis explaining natural wolf numerical responses in virtually all studies of wolf-prey systems in North America. Commonly cited reviews of this relationship, however, show considerable variability in growth rates and wolf densities relative to ungulate biomass (Keith 1983; Fuller 1989).

Prey availability and vulnerability can be significant in determining potential numerical responses by wolves. For example, deer, which are highly vulnerable and spatially available to wolf predation, would be expected to yield a "tighter" numerical response by wolves than would sheep or moose which are less spatially available and less vulnerable (Sumanik 1987; Dale et al. 1995). Those migrant ungulate populations also inherently vulnerable to wolf predation confound the predicted numerical response because they may at times yield a "tight" numerical response when concentrated on wintering areas (Parker 1973) or a "loose" numerical response when they move away from territorial wolf packs (Ballard et al. 1997).

The range of potential positive growth rates exhibited by wolf populations is larger than for most other large mammal species. Single year, finite annual growth rates as high as 2.5 have been reported for wolf populations recovering from intensive human exploitation (Ballard et al. 1987; Hayes 1995). However, in the absence of intensive exploitation, most wolf populations do not increase greater than about 50% per year (i.e., $\lambda = 1.5$; Table 6).

In developing PredPrey we recognized that the numerical response of wolves to prey densities was a significant function, possibly containing a large portion of the model's total sensitivity to change. From the literature review, we also realized that the numerical response might often be ill defined. To define the PredPrey Wolf Growth Function (i.e., numerical response) we first expanded on Keith's (1983) data set of 7 studies to include 12 studies from which wolf

population growth rates and ungulate densities were available (Table 6). We chose periods from within those studies that did not exhibit lags from high prey vulnerability during the early years of rapid ungulate declines and avoided data associated with human exploitation rates greater than 20%.

We tested a number of functions to fit the data set, including linear (Keith 1983), polynomial, and logarithmic fits. During simulations of moose-wolf systems, we observed that small changes in wolf finite growth rates in the region of λ = 0.9–1.1 could result in dramatically different moose population responses when moose production and mortality were closely balanced with wolf kill rates. The relationship of wolf growth rates to ungulate biomass in the data set is also the most variable in the region λ = 0.90–1.1 (Fig 6); therefore, the predictive value is inherently poor in this region for any function that is fit to the empirical data. Furthermore, predator-prey systems where both wolves and their prey are harvested at or below sustained yields often exhibit wolf densities that are near the wolf carrying capacity and therefore finite wolf population growth rates frequently may be near 1.0. As a result, the real world data that is entered for simulations in PredPrey will, more often than not, be drawn from systems with inherently poor predictability.

The best fit to the available data points ($r^2 = 0.80$, Fig 6) and the estimate of the associated variance were determined with the Microsoft®Excel for Windows®95 solver, minimizing squared differences between the function and the empirical data. We used a modified Michaelis-Menten Function (Fryxell 1991; Messier 1994) of the form $Y(x) = a(x-c)/(b+x)$. The variance $(\sigma^2(x))$ was estimated as $exp(d_0+d_1x+d_2x^2)$. We estimated 6 parameters, 3 from the function and 3 from the variance yielding 12-6 = 6 degrees of freedom (J Ver Hoef, pers commun). The best fit function was $Y = 1.55(X-24.82)/(48.49+X)$. The parameters c and b change the shape of the function, a is the asymptotic wolf finite growth rate (i.e., λ = 1.55), $Y(x)$ is the unadjusted predicted finite growth rate, and x is the total relative ungulate biomass index per wolf.

Based upon our knowledge of the variability in potential numerical responses and in the empirical data set, we viewed the best fit function as one possibility among an infinite number of similar functions. To accommodate those infinite possibilities, we created a subroutine to generate up to 256 iterations of a single model simulation by randomly selecting wolf growth rates from around the best fit function within prescribed prediction limits. Prediction limits were calculated as a scaled t-distribution centered on the best fit function $Y(x)$ with the estimated variance $(\sigma^2(x))$.

To derive a stochastic estimate of the finite growth rate at any given value of ungulate biomass (i.e., x value), the model randomly selects a value within the prediction limit generated for that x value. Because the empirical data are more highly variable in the mid section of their distribution relative to ungulate biomass, the range of possible functions to fit the data is also greater; hence, the stochastic function produces more variable finite growth rates as the predicted y value approaches 1.0. This function then fits the reality that the predictability of wolf finite growth rates is lowest when ungulate biomass and wolf density are near what would appear to be equilibrium.

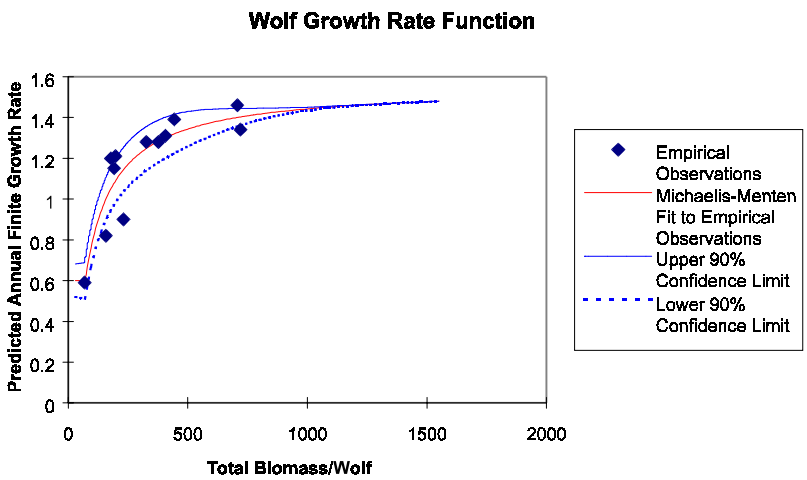

Figure 6 The modified Michaelis-Menten Function used in PredPrey to control the wolf numerical response to changes in the prey biomass availability. The Wolf Growth Function extracts values from a *t*-distribution centered on the best fit line. The dotted lines reflect the 90% confidence limits for that distribution.

In selecting data points for our empirical data set we purposefully excluded data that exhibited lags, i.e., where the numerical response was inconsistent with the trend in prey populations. Lags can result during prey declines when 1) increased vulnerability of prey results in increased prey availability and wolf populations may temporarily remain stable or even increase (Mech 1977; Peterson and Page 1988) or 2) when wolves at least partially switch to utilization of alternate prey and thereby maintain higher densities than could be supported by the declining primary prey (Mech 1977; Fuller 1989). Increased prey vulnerability is often associated with severe winter weather (Mech and Karns 1977; Peterson 1977; Mech et al. 1995) and, therefore, wolves may numerically increase following severe winters at a higher rate than would be predicted by prey abundance, even if prey are stable or increasing.

In PredPrey we model the existence of lags by adding a random value *D* (ranging from 0.04–0.10) to the wolf finite growth rate predicted by the Wolf Growth Function when the weather severity index is equal to or greater than 2.0 (i.e., simulated severe winter). This increase occurs regardless of the trend in the current prey population. In cases where the Wolf Growth Function predicts a declining wolf population, the lag adjustment may not result in increasing wolf numbers, but rather a reduced rate of decline. During simulated mild or moderate winters (i.e., weather severity index <2.0), $D = 0$.

PredPrey provides a chart illustrating the observed relationship between wolf density and ungulate biomass as a reality check to gauge simulated wolf population growth with empirical data (Fig 7). Wolf densities in PredPrey are generated from the Wolf Growth Function with no mechanism to ensure that resulting densities fall within the 90% prediction interval of the wolf density regression; i.e., the Growth Function and the Wolf Carrying Capacity regression are independent. In simulations where wolf populations are regulated by harvest, predicted wolf densities may commonly fall below the prediction interval of the empirical data set

represented in the wolf density regression. Lags in the wolf numerical response may result in wolf density values that lie above the prediction interval.

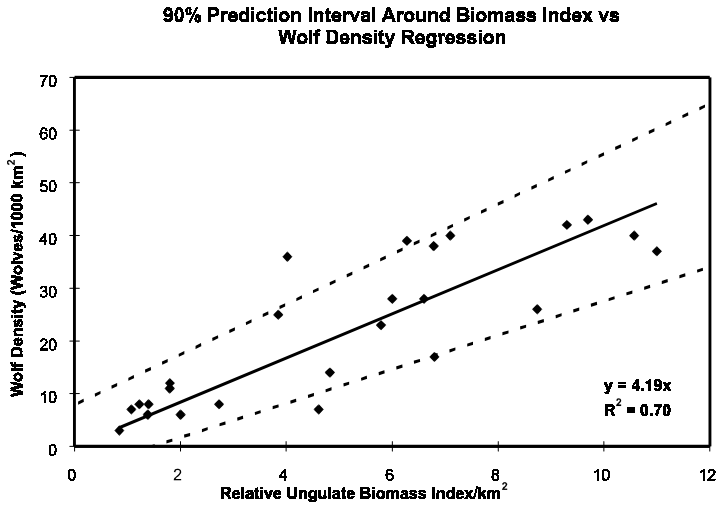

Figure 7 Regression of wolf density against an index to ungulate biomass using data from 25 studies of North American wolf-prey systems (modified from Fuller 1989). Dotted lines represent a 90% confidence limit around the observations. We consider the area between the upper and lower confidence limit to represent an estimate of wolf carrying capacity as limited by food.

The concept of an intrinsic social limitation to wolf population size has been offered as an explanation for the failure of some wolf populations to continue to increase despite abundant prey (Pimlott 1970, cited by Packard and Mech 1980), but Packard and Mech (1980) argued that apparent social restriction on wolf population growth was the "proximate cause of numerical change which is ultimately controlled by food." More recently, Messier (1994) reviewed 27 studies where moose were the primary prey of wolves and found a Type II numerical response of wolf populations to increasing moose density, again indicating spatial (i.e., social) restrictions on wolf densities (Messier 1995). Regardless of the food/social limits, wolf density limits do not seem to be strongly dependent upon prey type (Table 7).

Dynamic prey vulnerability is probably responsible for many of the inconsistencies seen in the wolf density vs. ungulate biomass regression. Vulnerability to wolf predation varies among species (Mech 1977; Carbyn 1983; Dale et al. 1995) and may reflect how social organization of the prey affects spatial overlap with wolves and therefore encounter rates (Huggard 1993*a*). For example, in moose-caribou-wolf systems, wolf densities may be dependent on nonmigratory moose densities if moose are vulnerable and caribou are only seasonally available (Seip 1992; Ballard et al. 1997), but may be more closely linked to caribou if moose are in good condition and relatively invulnerable to wolf predation even if caribou densities are periodically low (Dale et al. 1995).

To model dynamic prey vulnerability PredPrey allows the user to place an upper limit on wolf density, regardless of the ungulate biomass-wolf density relationship. When enabled, the function progressively adjusts wolf population growth rates as the simulated wolf population

approaches the user-entered limit (Fig 8). That allows the user to experiment with spatial/social restrictions to wolf population growth, to simulate the periodic presence and absence of migratory caribou in multi-prey systems, or to simulate wolf populations regulated by human activities.

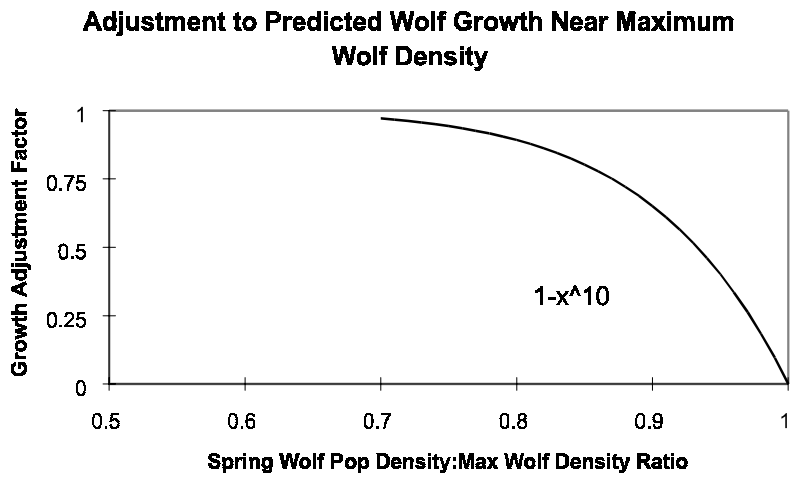

Figure 8 Function to limit wolf densities to a specified maximum value. As wolf density approaches the specified value, predicted finite growth rates are multiplied by the growth adjustment factor, depicted here on the *Y* axis. The specified maximum value is entered by the user.

Within a species, vulnerability may be related to age, physical condition, or breeding status, (Huggard 1993*b*; Mech et al. 1995). For example, winter moose calves may be more vulnerable to wolf predation than adult moose (Peterson et al. 1984), but winter caribou calves may not (Davis et al. 1991; Ballard et al. 1997). Undoubtedly those relative vulnerabilities change from population to population and even temporally within populations as a function of shifts in population age structure. To fit a variety of inherent vulnerability patterns to a particular simulation, PredPrey allows the user to adjust the relative vulnerability of different sex and age classes within the simulated Current Prey Population (Appendix A).

MODEL TESTING

The documented case history begins in 1965 with an estimated moose population of 23,000 moose within the 17,000-km^2 study area (Gasaway et al. 1983). The moose population declined to a low of approximately 2800 moose by 1975, then increased to approximately 11,200 by 1992 (Boertje et al. 1996). During the decline, winter weather was severe during 1965–1966, 1966–1967, 1970–1971, and 1974–1975, as measured by snow depth and persistence of snow late into the spring. Total snowfall was not excessive in 1967–1968 or 1971–1972, but during both years snow accumulation persisted through April and was greater than 45 cm on 20 April. Weather was thought to be a major determinant initiating the decline in 1965 and accelerating the decline in 1970. During both winters nearly 50% of the estimated moose population may have died before spring (Bishop and Rausch 1974). Overbrowsing probably contributed to the initial decline, but based on indices of productivity, density-dependent effects were not apparent after 1967 (Gasaway et al. 1983).

Beginning in winter 1975–1976, wolves were reduced in the study area by shooting from aircraft. Intensive wolf control continued through the winter of 1979–1980, and at a less intense level until spring 1982. The moose population began increasing in 1976 and during the next 13 winters (1976–1988) winter severity was near or below average. Beginning in 1989 and persisting through winter 1992–1993, winters were severe with deep, persistent snow.

The change from a rapidly declining moose population (1965–1975) to a rapidly increasing population (1976–1989) was probably accompanied by a dramatic shift in the population age structure. Gasaway et al. (1983) estimated 41% of the cows in the 1972–1974 population were ≥11 years of age and approximately 40% of those cows were dying annually. They found a higher proportion of young and middle-aged animals after 1976. We suspect that younger age structure, in the absence of severe weather, reduced the vulnerability of moose to wolf predation, contributing to the rapid increase in moose numbers.

The PredPrey simulations closely reproduced changes in the moose population documented in the case history (Fig 9). That does not validate PredPrey as a predictive model, but rather demonstrates how it can be adapted to produce desired population responses relative to a particular empirical data set. That characteristic is a necessary first step in creating predictive simulations, but additional simulations of different types of predator-prey systems are obviously needed to assess the model's potential for general application.

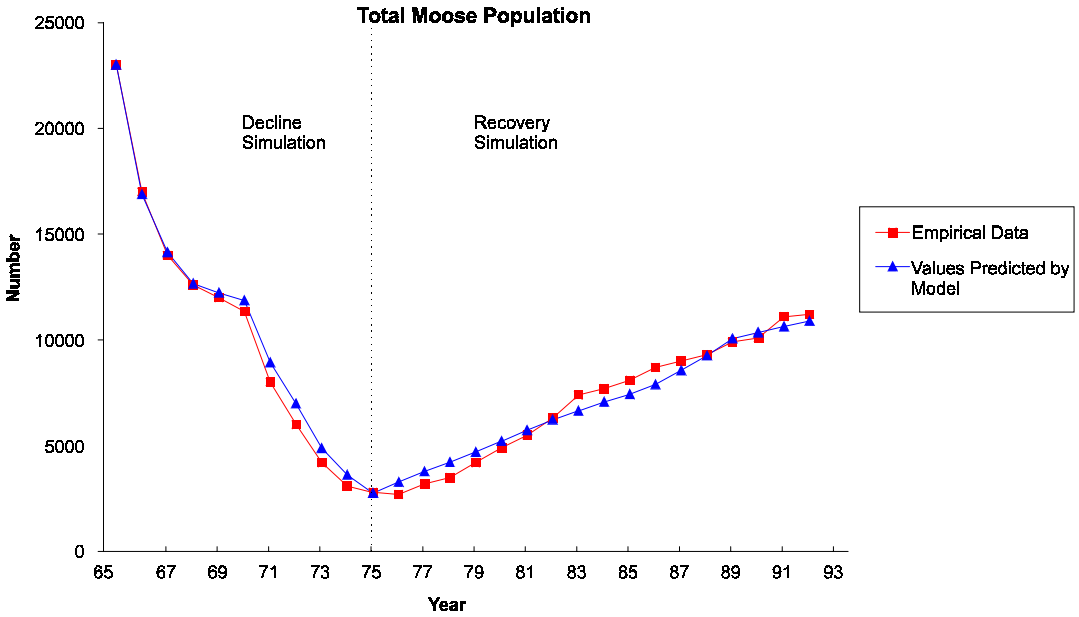

Figure 9 Comparison of empirical data (Gasaway et al. 1983; Boertje et al. 1996) with PredPrey simulation of moose population response to severe weather, density dependence, wolf predation, hunting and wolf control in Alaska Unit 20A, 1965–1993

The simulated decline and increase also closely track the empirical wolf population data. However, a discrepancy in the timing of the wolf population decline is apparent in the simulation data from 1972 to 1975 (Fig 10). This discrepancy results from a PredPrey Function that dampens the "lag" in the numerical response of wolves to declining prey. When the Current Prey population is declining, the function projects the numerical response of wolves based on the linear trend of the Current Prey as established by the present year and the year preceding the present year. This projection results in a "tight" response of wolf numbers to changes in total prey biomass. If Alternate Prey exist and compose a large portion of the total biomass, the numerical response becomes looser.

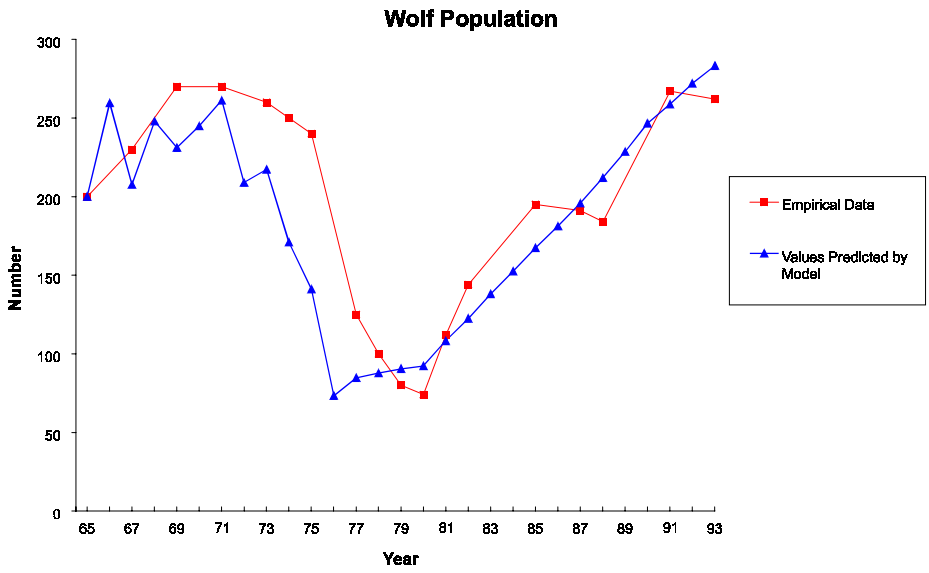

Figure 10 Comparison of empirical data (Gasaway et al. 1983; Boertje et al. 1996) with PredPrey simulation of wolf population response to changes in moose density, harvest by humans, and wolf control.

Lags have often been reported for the numerical response of wolves to changing prey density (Packard and Mech 1980), but wolves also have the ability for immediate numerical responses through dispersal (Parker 1973; Dale et al. 1995). To model the existence of lags, PredPrey contains a function which induces a lag in the wolf numerical response when weather is severe. In real systems, however, lags can be induced by changes in prey species' vulnerability resulting from changing age structure or prey species' composition (Seip 1992), even in the absence of severe weather. Because weather was not severe, we suggest the 1972–1975 lag in the numerical response of wolves in Unit 20A reflects an increase in the vulnerability of moose to wolf predation caused by changes in the moose population age structure. The relative old age of harvested cow moose and the high predation rate by wolves on those cows during the declining phase (Gasaway et al. 1983) support that hypothesis. The current version of PredPrey does not allow such nonweather-related lags; however, we envision a more flexible lag function for the wolf numerical response in future versions of the model to allow the user to select a variable lag.

For both the decline and recovery simulations, we manipulated weather severity indices to reflect increased natural mortality rates associated with severe weather events. In doing so we attempted to reproduce trends in sex and age composition ratios that compared favorably with the empirical data. Reproducing the moose population response alone is inadequate if management decisions are also guided by desired male:female ratios or if allowable harvest rates are to reflect potential recruitment to the managed population.

The PredPrey simulations tracked the general trend of sex and age composition ratios from the case history data (Fig 11) but notably diverged from empirical calf:ratios during the

mid-1980s and diverged from empirical bull:cow ratios during the early 1970s. The higher calf:cow ratios were probably the result of diverging twinning rates between the empirical and simulated populations. The current version of PredPrey accepts an initial estimate of twinning rates that remain constant unless the prey population increases to a level invoking density-dependent effects.

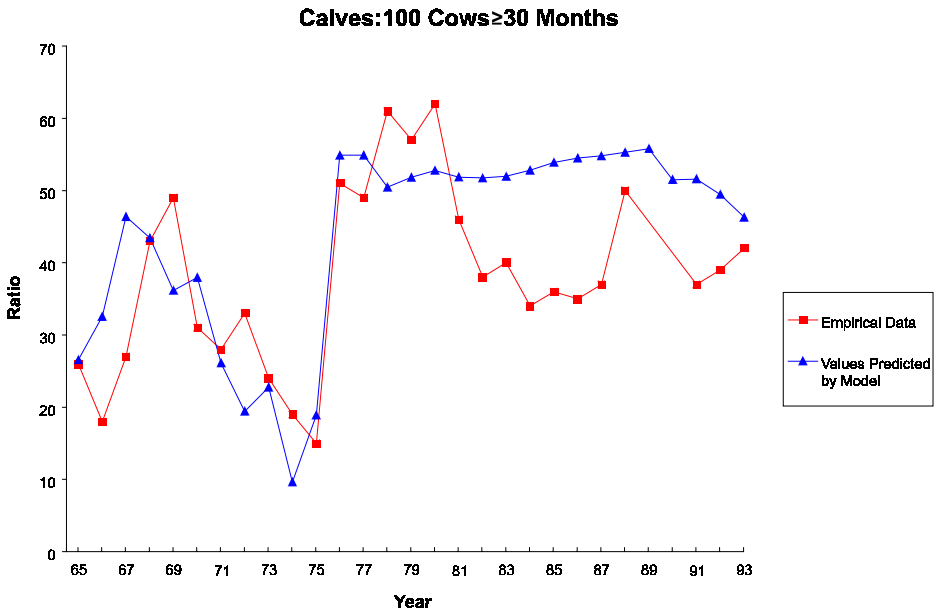

Figure 11 Comparison of empirical data (Gasaway et al. 1983; Boertje et al. 1996) with PredPrey simulation of changes in calves/100 cows ≥30 months for Alaska Unit 20A, 1965–1993

Gasaway et al. (1983) reported twinning rates of 32% during 1977 and 1978, but twinning declined to 10–16% by the late 1980s (Boertje et al. 1996). We initialized the recovery simulation with twinning rates of 25% to reflect the higher rates reported by Gasaway et al. (1983) during the early recovery. Therefore, the PredPrey simulation probably overestimated twinning during the mid to late 1980s. Almost identical population responses were maintained because we manipulated overwinter mortality in the PredPrey simulations. That is in part reflected by the lower yearling survival in PredPrey compared with the empirical data during the early 1980s (Fig 12). The higher predicted calf:cow ratios and lower yearling survival produced by PredPrey resulted in similar numbers of yearling recruits for both the PredPrey and empirical data sets. However, this example points out the need to conduct short-term simulations in PredPrey and illustrates how rapidly changing real world population characteristics may not be accurately reflected in long-term simulations.

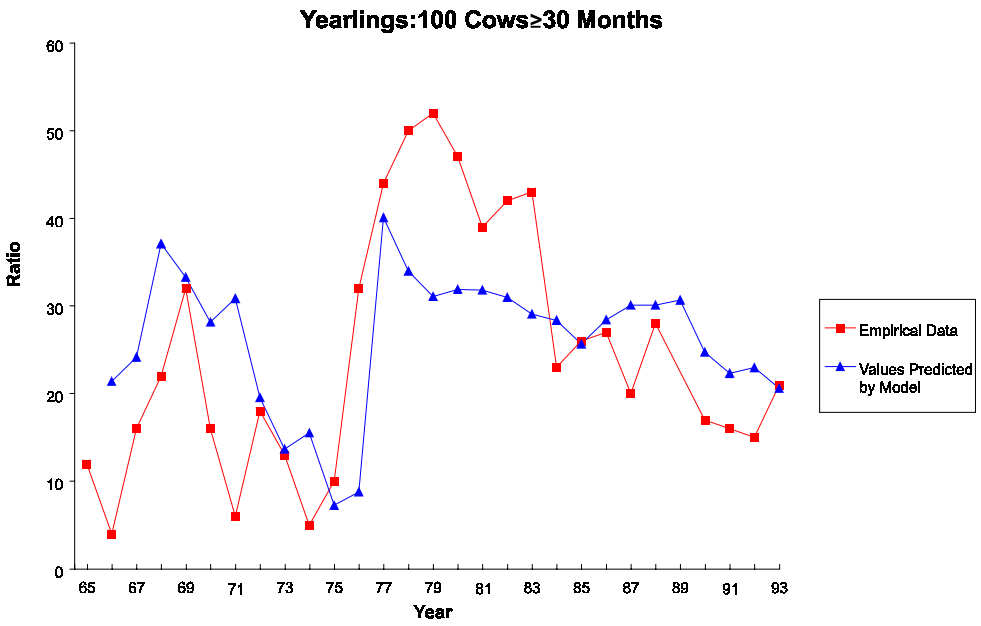

Figure 12 Comparison of empirical data (Gasaway et al. 1983; Boertje et al. 1996) with PredPrey simulation of total yearlings/100 cows ≥30 months in Alaska Unit 20A, 1965–1993

Inconsistencies in simulated vs. empirical bull:cow ratios during the early 1970s possibly reflect the small sample sizes and incomplete survey coverage characteristic of surveys from that period. Intuitively, we would expect higher bull:cow ratios than those reported in the empirical data because the moose population was aggressively harvested between 1971 and 1974 (mean harvest rate = 12%/yr) and cows composed an average of 42% of those harvests. Empirical bull:cow ratios from years when survey coverage was more complete (1978, 1982, 1984, 1988, 1990, 1991, 1992) compare favorably with those predicted by PredPrey (Fig 13).

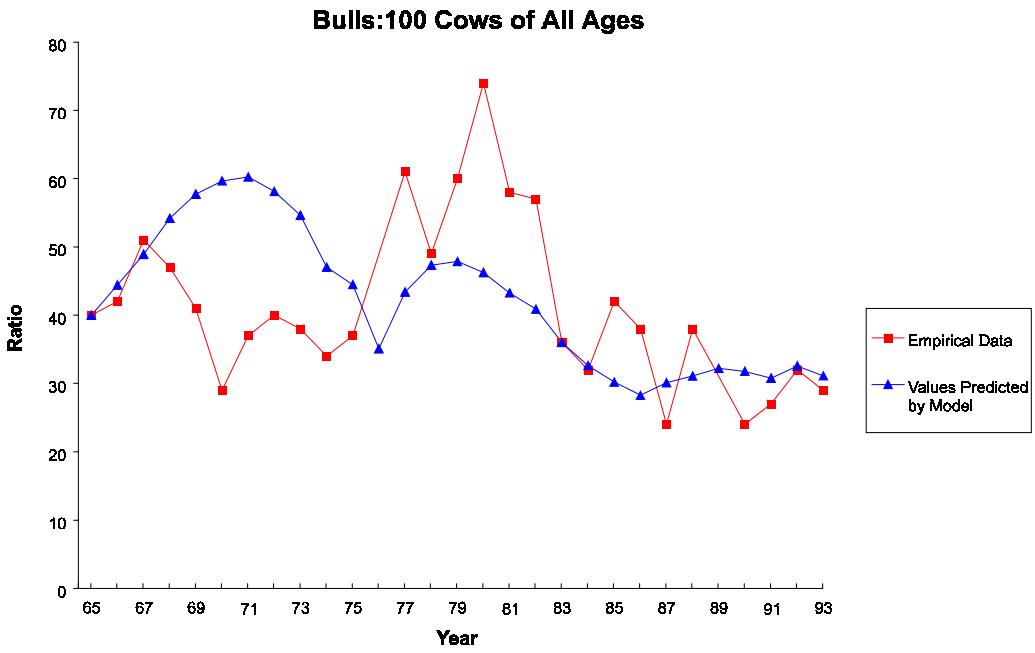

Figure 13 Comparison of empirical data (Gasaway et al. 1983; Boertje et al. 1996) with PredPrey simulation of bulls/100 cows in Alaska Unit 20A, 1965–1993

Introducing stochastic weather clearly illustrated the potential significance of weather on the natural mortality of prey populations. Stochastic weather simulations were based on probabilities of severe weather reported in the empirical data of Gasaway et al. (1983) and Boertje et al. (1996). The variability in the stochastic population responses indicates the population decline was not inevitable but a function of weather timing and severity given the managed combination of hunting and predation (Fig 14). In contrast, during the recovery simulation, all of the iterations showed a consistent increase for the period 1975–1982. That simulation indicates that despite variable weather, the wolf control program reduced the primary factor (i.e., wolf predation) limiting moose population growth during that period. However, the variable response shown by the simulation after wolf control ceased indicates the long-term moose population recovery was the result of continuous favorable weather and the short-term wolf control program, by itself, may not have resulted in the total increase in moose numbers documented by the case history (Fig 15).

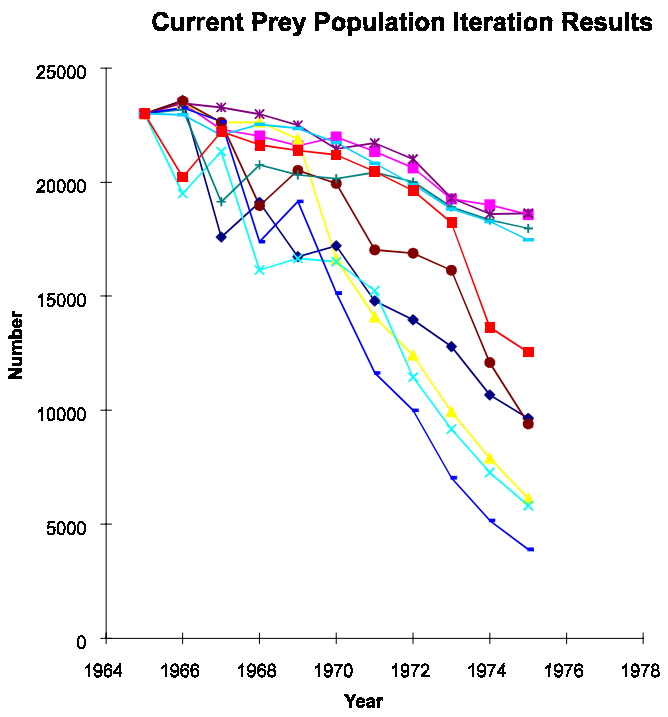

Figure 14 Moose population responses resulting from stochastic weather and wolf population growth functions enabled for the decline phase of the Unit 20A moose population 1965–1975. Other inputs were identical to those that produced the deterministic response depicted in Figure 9.

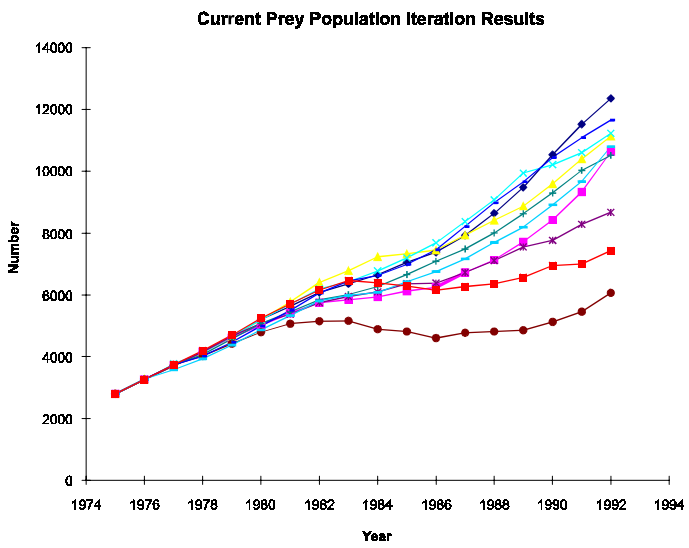

Figure 15 Moose population response resulting from stochastic weather and wolf growth functions enabled during PredPrey simulation of recovery of the Unit 20A moose population 1975–1993. Other inputs were identical to those that produced the deterministic response depicted in Figure 9.

At the date of this report, PredPrey was in the final stages of development but remained an incomplete prototype. Although the single test presented here is encouraging because it closely mimics moose population response in a complex predator-prey system, many model functions can only be completed and refined by testing the model against empirical data sets from a variety of predator-prey systems. Sensitivity testing has not been conducted and will be required to reveal idiosyncrasies that may adversely affect the model's ability to simulate certain natural systems. In addition, documentation of the model has not been completed. Full documentation would include an explanation for each of the 390 predator and prey population characteristics calculated during each PredPrey run. Most of those characteristics are not presented in the PredPrey charts or vital statistics tables but are available to the user in Microsoft®Excel spreadsheets within the 6 submodels.

We discuss some of the most significant PredPrey functions in this final report, but were unable to expand upon the details of many other functions. Brief explanations are contained in the PredPrey User's manual, attached as Appendix A. We refer readers to that manual for discussion of the following additional PredPrey functions and characteristics:

Subject	Page
Annual Model Cycles	54
Bear Predation	60
Density Dependence	70
Alternate Prey	71
Weather	75
Harvest of Current Prey	76
Harvest of wolves and simulated wolf control	78
Harvest of Bears	78
Productivity of the Current Prey	80
Age Structure of the Current Prey	81
Prey Vulnerability	82
Survivorship	112
Predation Rates	118
Yield Curve	123

An objective of this project was to complete a separate report on moose–wolf dynamics in Unit 20B West. We made progress on that report and compiled and presented data in an earlier progress report (McNay 1993). Time constraints involved in developing the modeling portion of this project prevented us from making further progress on that objective, and we refer readers to McNay (1993) for the data analysis and discussion.

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PREPARED BY:

Mark E McNay
Wildlife Biologist III

Robert A DeLong
Analyst Programmer III

SUBMITTED BY:

Kenneth R Whitten
Research Coordinator

APPROVED BY:

_____
Wayne L Regelin, Director
Division of Wildlife Conservation

_____
Steven R Peterson, Senior Staff Biologist
Division of Wildlife Conservation

Table 1 List of PredPrey submodel worksheets and the primary category of calculations contained in each worksheet. Worksheets are accessed from the Main Menu.

Submodel Worksheet	Calculation Categories
Primary Population	Contains calculations for the ungulate prey population size and composition, prey vulnerability, survival, wolf consumption rates, density-dependent effects and environmental effects. This worksheet also contains population values for predators imported from other worksheets. Calculations in this worksheet are based on a "harvest year" 1 Nov–30 Oct.
Postcalving Mortality	Contains calculations based on the "biological year" 1 May–30 Apr for the ungulate prey species. Calculates productivity of the Current Prey species and summer mortality of Current Prey by grizzly bears. Mortality attributed to various causes for the biological year is calculated for inclusion in Distribution of Mortality Charts.
Wolf Population and Harvest	Contains calculations for simulated public harvest and wolf control harvest of wolves, calculation of pack numbers and sizes, and autumn and spring wolf population sizes.
Alternate Prey and Biomass	Contains calculations for total ungulate biomass that is present in the simulated system, including alternate prey and nonungulate wolf food biomass. Predation functional responses and numerical responses that are dependent upon ungulate biomass are also calculated within this submodel.
Prey Weight Table	This submodel stores the weight values for different sex and age classes of each of the potential ungulate prey species, calculates the biomass index values from those weights, and stores the consumption coefficients used to estimate inedible portions of ungulate carcasses. Users may modify the Prey Weight values through the Advanced Inputs Dialog box.
Optional Predators	Contains calculations for changes in Optional Predator populations and calculates the mortality of the various sex and age classes of Current Prey resulting from predation by the Optional Predator.
Current Prey Harvest	Contains calculations for both user and model generated harvest of the Current Prey.

Table 2 Observed natural mortality rates among moose and caribou

Sex/Age/ Species	% Total natural mortality	% Nonpredation mortality	Severe weather[a]	Time span (yr)	Location	Reference
Bull moose	10–22[b]	--	0	10	Southcentral Alaska	Modafferi and Becker 1997
Bull moose	71	--	+	1	Southcentral Alaska	Modafferi and Becker 1997
Cow moose	6–11[b]	--	0	10	Southcentral Alaska	Modafferi and Becker 1997
Cow moose	35	--	+	1	Southcentral Alaska	Modafferi and Becker 1997
Calf moose, 0–12 months	67	--	0	8	Southcentral Alaska	Ballard et al. 1991
Calf moose, 5–12 months	11	--	+[c]	3	Southcentral Alaska	Ballard et al. 1991
Adult cow moose	5	--	0[c]	10	Southcentral Alaska	Ballard et al. 1991
Yrlg cow moose	6	--	0	5	Southcentral Alaska	Ballard et al. 1991
Yrlg bull moose	9	--	0	3	Southcentral Alaska	Ballard et al. 1991
Cow moose	9	0	0	3	Yukon	Larsen et al. 1989
Calf moose, 0–12 months	81	7	0	3	Yukon	Larsen et al. 1989
Cow moose	3	2	0	6		Bangs et al. 1989
Moose older than 6 months	3	3	0	4	Colorado	Kufeld and Bowden 1996
Cow caribou, 8–12 months	3	--	0	9	Interior Alaska	Davis et al. 1991
Yearling cow caribou	2	--	0	9	Interior Alaska	Davis et al. 1991
Adult cow caribou	7	--	0	9	Interior Alaska	Davis et al. 1991
Yearling bull caribou	19	--	0	9	Interior Alaska	Davis et al. 1991
Adult bull caribou	19	--	0	9	Interior Alaska	Davis et al. 1991
Adult cow caribou	16	--	+	4	Interior Alaska	Valkenburg 1997
Calf caribou, 0–12 months	47	4	0	4	Interior Alaska	Boertje and Gardner, in press
Calf caribou, 4–16 months	57	--	+	1	Interior Alaska	Boertje and Gardner, in press
Calf caribou, 4–16 months	17	--	0	6	Interior Alaska	Boertje and Gardner, in press
Adult female caribou	22	--	+	4	Interior Alaska	Boertje and Gardner, in press
Adult female caribou	8	--	0	5	Interior Alaska	Boertje and Gardner, in press

[a] 0 = no severe weather; + = severe weather associated with reported mortality rates.
[b] Range of values = 95% CI.
[c] One winter of 3 was severe.

Table 3 Wolf consumption rates reported from 15 North American studies of winter predation rates by wolves (modified from Ballard et al. 1997 and Fuller 1989)

Location	Major Prey	UBIPW[a]	Winter consumption rate		Reference
			kg/wolf/day	kg/kg wolf/day	
Ontario	Deer	112	2.9	0.10	Kolenosky 1972
Alberta	Bison	152	5.3	5.3	Oosenbrug and Carbyn 1982
Yukon	Sheep	153	3.0	0.08	Sumanik 1987
Minnesota	Deer	161	2.0	0.06	Fuller 1989
Quebec	Moose	162	2.2	0.07	Messier and Crete 1985
Minnesota	Deer	178	2.9	0.10	Mech 1977
Isle Royale	Moose	225	7.2	0.22	Peterson 1977
Alberta	Moose	231	5.5	0.14	Fuller and Keith 1980
Isle Royale	Moose	264	4.9	0.15	Peterson and Page 1988
Arctic Alaska	Caribou Moose	267	5.3	0.12	Ballard et al. 1997
Denali Park	Moose	334	4.5	0.11	Haber 1977
Manitoba	Elk	336	6.8	0.21	Carbyn 1983
Alaska	Moose	345	4.8	0.12	Peterson et al. 1984
Minnesota	Deer	400	2.9	0.09	Fritts and Mech 1981
Alaska	Moose	659	7.1	0.18	Ballard et al. 1987

[a] Ungulate Biomass Index per wolf.

Table 4 Estimated annual kill rates by wolves on deer

Location	Estimated annual kill rate[a]	Reference
Minnesota	15–18	Mech and Karns 1977
Vancouver Island	16–33	Hebert et al. 1982
Southeast Alaska	26	Persons et al. 1996
Minnesota	19	Fuller 1989
Minnesota, Ontario, and Manitoba	17[b]	Keith 1983

[a] Number of animals killed per wolf per year.
[b] Includes deer and elk.

Table 5 Estimated winter (Oct–Apr) kill rates by wolves on moose, bison, and elk

Location	Species	Estimated annual kill rate[a]	Reference
Southcentral Alaska	Moose, Caribou	7.2	Ballard et al. 1987
Interior Alaska	Moose, Caribou	7.6	McNay 1990
Kenai Peninsula, Alaska	Moose	5.0	Peterson et al. 1984
Northeast Alberta	Moose	4.0	Fuller and Keith 1980
Manitoba	Elk	≤15	Carbyn 1983
Alberta and NWT	Bison	3.0	Carbyn et al. 1993

[a] Estimated number of animals killed per wolf calculated from mean pack size and mean pack kill intervals, unadjusted for prey size. Where kill rates were determined from short, mid, or late winter periods, or from repeated sampling periods, results were extrapolated to the 212-day period Oct–Apr.

Table 6 Wolf population annual finite growth rates and corresponding Ungulate Biomass per wolf values used to construct PredPrey Wolf Growth Function (i.e., numerical response)

Prey species	UBIPW[a]	WFGR[b]	Estimated wolf density[c] (wolves/1000 km^2)	Wolf exploitation rate (%)[d]	Location	Reference
Moose	69	0.59	8.5	7	Interior Alaska	Whitman and McNay, 1997
Moose	157	0.82	57.6	0	Isle Royale	Peterson and Page 1988
Deer, Moose	178	1.20	24.2	--	Algonquin Park, Ontario	Pimlott et al. 1969, Theberge and Strickland 1978, cited by Keith 1983
Moose	192	1.15	50.2	0	Isle Royale	Peterson 1977
Moose	198	1.21	5.5	8	Alberta	Fuller and Keith 1980
Moose, Caribou, Sheep	231	0.90	8.1	0	Denali Park, Alaska	L Adams, pers commun, 1990–1993 data
Moose, Caribou	327	1.28	7.5	12	Interior Alaska	Boertje et al. 1996
Moose, Caribou	377	1.28	6.1	0	Denali Park, Alaska	L Adams, pers commun, 1986–1989 data
Deer, Moose	406	1.31	16.8	17	Minnesota	Fritts and Mech 1981, cited by Keith 1983
Moose	444	1.39	19.9	0	Isle Royale	Krefting 1951, Mech 1966, Peterson 1977, cited by Keith 1983
Moose	708	1.46	11.0	--	Alberta	Bjorge 1979, cited by Keith 1983
Moose	720	1.34	6.0	--	Arctic Alaska	Stephenson and Sexton 1974, cited by Keith 1983

[a] Ungulates were assigned a relative biomass index of 6, 2, and 1 for moose, caribou and deer, respectively. The number of ungulates multiplied by the appropriate biomass index, then divided by the number of wolves yields the Ungulate Biomass Index per wolf (UBIPW; Keith 1983).
[b] Wolf finite Growth Rate.
[c] Approximate mean density between high and low densities estimated during growth rate period.
[d] Proportion of winter wolf population dying from human-caused mortality (e.g., hunting, trapping, vehicle accidents, poaching, etc.).

Table 7 Summary of highest gray wolf densities reported within a variety of North American predator-prey systems

Location	Reference	Prey type and diversity	Wolf density (wolves/1000 km^2)
Arctic Alaska	Ballard et al. 1997	Caribou, Moose	8
Interior Alaska	Boertje et al. 1996	Caribou, Moose, Dall Sheep	16
Southeast Alaska	Persons et al. 1996	Deer	39
Minnesota	Fuller 1989	Deer, Moose	59
Northeast British Columbia	Bergerud and Elliot 1990	Moose, Elk, Sheep, Caribou, Deer	39
Northcentral Canada	Parker 1973	Caribou	49
Yukon	Hayes et al. 1991	Moose, Sheep	12
Southwest Manitoba	Carbyn 1977	Elk, Deer, Moose	43
Southern Quebec	Potvin et al. 1992	Deer	28
Island populations:			
Isle Royale, MI (544 km^2)	Peterson and Page 1988	Moose	92
Coronation Island, AK (78 km^2)	Klein 1995	Deer	167

Files not included in this format:

APPENDIX A PredPrey User's Guide (Draft)

APPENDIX B Model calculated values and formulas

APPENDIX C Screen prints of user interface