Alaska Department of Fish and Game
Division of Wildlife Conservation

Federal Aid in Wildlife Restoration
Research Progress Report
1 July 1996-30 June 1997

Development and Testing of a General Predator-Prey Computer Model for Use in Management Decision-Making

Mark E McNay
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Grant W-24-5
Study 1.46
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RESEARCH PROGRESS REPORT

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

AUTHORS: Mark E McNay and Robert A DeLong

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SUMMARY

Progress continued on development of a general predator-prey computer model, named Predprey. The original model prototype was converted to Microsoft®Excel for Windows®95 from Lotus®1-2-3 for DOS®. Five submodels were arranged on individual Microsoft®Excel worksheets to allow expansion of model functions. Microsoft®Visual Basic® programming was used to create a user interface that simplifies model inputs and allows the user to progressively increase complexity of simulations. Model variables are entered by the user through dialog boxes that use standard Windows®95 controls. Predprey is designed as a self-tutorial program with an on-line user's manual accessible from any submenu within the model.

Predprey is a discrete-time model and the user can select either stochastic or deterministic weather parameters. Model outputs include 2 tables and 14 charts depicting different aspects of predator and prey population interactions. Model functions include calculation of predator and prey population changes over a 20-year period, predation rates, predator functional responses, stochastic weather effects on natural mortality, differential prey vulnerability, effects of user selected harvests, wolf (*Canis lupus*) numerical responses, and density-dependent effects on ungulates. 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.

Key words: bears, computer model, density dependent, functional response, numerical response, predator-prey, stochastic weather, ungulate, wolves.

CONTENTS

BACKGROUND

In 1991 a comprehensive 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 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.

Often managers have only rough estimates for population size, sex and age ratios, predator numbers, and even harvest rates. Yet, they are required to make annual recommendations for seasons and bag limits, must often respond to public or media inquiries about the effects of predation versus hunting, and are routinely asked to defend their recommendations in front of advisory committees or the Board of Game. The purpose of this model is to help managers do those jobs more objectively with greater confidence and effectiveness.

In response to past controversy over predator-prey management, biologists in Alaska, other northern states, and the Yukon conducted significant research on large ungulate-large carnivore ecological systems. Advances in large prey-predator ecological research, and the wide availability and use of personal computers, created an opportunity to develop additional tools for management decisions.

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 follow 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 do not explicitly model those 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 1 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). Few are available to Alaskan managers in the form of easily used computer models that combine the potential effects of weather, predation, harvest, density dependence, prey vulnerability and population composition on allowable harvests.

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. 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 (Carbyn et al. 1993). Deer (*Odocoileus* spp.) population estimates in heavily forested areas are based on pellet group transects (Kirchoff 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 check stations (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 provided 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 by wolves and bears 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.

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 [*Bison bison*], and elk [*Cervus elaphus*]). Estimates of annual kill rates range from 15 to 33 deer/wolf/year (Table 1), and from 1.9 to 15 animals/wolf/winter among a variety of larger ungulate prey where winter wolf predation rates were measured (Table 2).

Table 1 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 2 Estimated winter (Oct-Apr) kill rates by wolves on moose, bison, and elk

Location	Species	Estimated winter kill rate[a]	Reference
Southcentral Alaska	Moose and Caribou	7.2	Ballard et al. 1987:Table 14
Interior Alaska	Moose and Caribou	7.6	McNay 1990
Kenai Peninsula, Alaska	Moose	5.0	Peterson et al. 1984:Table 5
Northeast Alberta	Moose	4.0	Fuller and Keith 1980:Table 6
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.

Black bears on 2 study sites in Southcentral Alaska killed an estimated 34% and 35% of neonatal moose calves (Schwartz and Franzmann 1991). Similarly, black bears killed an estimated 40% of moose calves in an Interior Alaskan study (Osborne et al. 1991). Predation by grizzly bears (*Ursus arctos*) on adult moose was documented in both Alaskan (Boertje et al. 1988; Ballard et al. 1990) and Yukon (Larsen et al. 1989) studies. Boertje et al. (1988) reported adult male grizzlies killed adult moose and caribou at a rate of approximately 1 kill per 26 bear days in spring and Ballard et al. (1990) reported adult grizzlies killed adult moose at a rate of 1 kill per 43.7 bear days in spring. Larsen et al. (1989) reported grizzly bears killed 2% to 3% of collared adult female moose in each of 3 years 1983-1985. Kill rates by grizzlies on moose calves were reported as 5.1, 5.4, and 5.3 calves per adult grizzly, respectively, in Yukon (Larsen et al. 1989), Eastcentral Alaska (Boertje et al. 1988), and Southcentral Alaska (Ballard et al. 1990). In Denali Park grizzly predation on neonatal caribou calves varied from 17% to 22% of calves produced between 1985 and 1987 (Adams et al. 1989).

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.

These 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 by allowing biologists to simulate potential consequences of different management actions in the presence of variable environmental conditions.

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

DEVELOPMENT OF PREDATOR-PREY MANAGEMENT MODEL

Model Conversion 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 to allow expansion of model functions. Using Visual Basic programming, a user interface was developed that 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 that use standard Microsoft® forWindows®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 increases user speed and enhances interpretation of results.

Model Characteristics

Predprey is a linear, 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. Therefore, when selected, stochastic weather is reflected in population responses throughout the model. With the deterministic function, the user has 2 options: 1) no adverse weather effects or 2) adverse weather events for selected years. Outputs from model calculations are portrayed in both tabular and graphic formats for a 10-year period. Population for both predators and prey are available with a push button option for a 20-year period.

The model simulates changes in population size, composition, allowable harvest, mortality, and productivity of 1 ungulate population called the Current Population. Changes in population size, determined by user selection of varying population growth rates (λ) of up to 7 additional ungulate populations, are calculated and recorded in a separate submodel. Those alternate prey populations simulate increased total ungulate biomass within the system. Changes in total ungulate biomass affect wolf population growth rates, which in turn 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 Current Population submodel, and begins on 1 November of the entry year. Overwinter predator- and nonpredator-caused mortality among the prey population are subtracted from the 1 November population on 1 May before production of neonates. Then the previous year's calf/fawn cohort, the previous year's yearling cohort, and the previous year's 2-year-old cohort advance in age 1 year on 1 May. Production is then added 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 October, to yield the starting population on 1 November for the next harvest year cycle. 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.

Changes in the Current Population are also calculated and reported based on the biological year 1 May to 30 April. The biological year cycle calculations enable calculation of mortality distribution among all sex and age classes from the peak annual population that results from calf/fawn production. The outputs from the biological year cycle are reported in bar and pie charts accessed by the Mortality and Harvest Chart button in the main menu.

Model Parameters

The term parameters refers to the general structure of equations which define fixed model functions. Parameter equations often were taken directly from published predator-prey studies or were modified by adding more recent data to published data sets. In some cases, we developed parameters to simulate functions for which there is general conceptual agreement, but little quantitative documentation (e.g., functional response curve).

For most parameters, the user provides input values for 1 or more variables contained in the parameter equations. Those input values modify the model output for a given model run. Population composition, mortality rate, harvest level, and production rate variables are examples of input values entered by the user.

Managing Model Complexity

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. The model can be difficult to use without considerable training.

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. For example, from the main menu users select either primary or advanced parameters. From the primary parameters dialog box, users input basic population characteristics with the option of selecting 1 to 6 additional dialog boxes for entry of variables associated with more complex simulations. From the Advanced Parameters dialog box, 4 push buttons allow access to more complex simulation variables. If the user does not select more complex dialog boxes, the variables associated with those dialog boxes are default values, and the effects of those variables are held constant.

Model States and Defaults

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 do not often create complex simulations. By entering the default state and then making desired changes only in the Initial Model Values dialog box, the user is assured that errors in entry for more complex variables will not affect the simulation.

Help Menu

Predprey is designed as a self-tutorial program. The entire text of the user's manual will be 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 reference table provides 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.

RESULTS AND DISCUSSION

DEVELOPMENT OF PREDATOR-PREY MANAGEMENT MODEL

Model Conversion and User Interface

During this reporting period progress was made in expansion and refinement of model parameters and in developing a user interface. The Lotus®1-2-3 for DOS® prototype (0.34MB) was converted to Microsoft®Excel for Windows®. The current Microsoft®Excel prototype (2.1MB) has the following system requirements:

Processor:	Pentium 60mhz (minimum) 90mhz (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

The user enters the model in the main menu (Fig 1) which provides push button controls to access 5 submodel worksheets and a prey weight reference table. The prey weight reference table is used to adjust Predprey to the physical characteristics of a particular prey population (Fig 2). For example, arctic caribou are smaller than Interior Alaskan caribou. Therefore, when simulating arctic caribou population response, the model should be adjusted to accurately reflect their smaller size because total ungulate biomass affects predation functions by wolves.

Data entry is accomplished through the Initial Model Values dialog box (Fig 2). Spinners, checkboxes, radio buttons, or push button controls are provided for input of 12 current prey variables, 5 wolf predation variables, 5 harvest variables, 5 neonate predation variables, and 4 environmental variables. The user does not have to enter each variable for each run but may recall (in the main menu [Fig 1]) a saved model state from a previous work session.

Model Characteristics

The model contains functions of varying complexity for zero to 5 predators, simultaneously. Wolf population simulations contain functions for variable predation rate, population growth, population structure, and harvest (Figs 3 and 4). Grizzly bear functions include a fixed predation rate and population growth and population objective functions (Fig 5). Black bears are treated only as predators of neonates. Other predators such as coyotes (*Canis latrans*), wolverine (*Gulo gulo*), lynx (*Lynx canadensis*), etc. can be included only as predators of neonates. The user may specify a fifth category of predator, the Optional Predator. Optional predators are customized by the user for predation rates among different sex and age classes of prey, for optional predator growth rates, and population objectives (Fig 6). Optional predators take on the predation characteristics of any predator desired by the user (e.g. mountain lions [*Puma concolor*], coastal brown bears, crippling loss by hunters, etc.).

Optional predator, grizzly bear, and wolf predation rates are further modified by default functional responses that can be customized by the user through the advanced model parameters dialog box (Fig 7). Each time a model recalculation occurs, the model outputs a summary of the results to 2 Vital Statistics tables (1 for current prey and 1 for all predator species, Figs 8 and 9, respectively). Each recalculation generates 14 charts, depicting different aspects of predator-prey relationships (Table 3).

Table 3 List of charts created by Predprey during each recalculation

Chart Name	Main menu access button	Chart display
10-year population	Prey	Displays Current Prey population change for 10 years
20-year population	Prey	Displays Current Prey population change for 20 years (Fig 10)
Sex/age ratios	Prey	Displays Current Prey population composition for 20 years
Predator population	Predator	Displays Predator and Prey Population change over 20 years (Fig 11)
Consumption rate	Predator	Displays seasonal per wolf per day consumption rates (Fig 12)
Prey density versus kill rate	Predator	Displays predator functional response to changes in total population density (Fig 13)
Neonate density	Predator	Displays predator functional response to changes in neonate density
Predation rate	Predator	Displays proportion of Current Prey population killed by wolves as a function of Current Prey density
Harvest	Mortality and harvest	Displays Sex composition of Harvest (Fig 14)
Mortality distribution	Mortality and harvest	Pie charts depicting distribution of Current Prey Mortality among all mortality factors (Fig 15)

Chart Name	Main menu access button	Chart display
Mortality	Mortality and harvest	Bar chart depicting annual distribution of mortality over 10 years compared with change in Current Prey spring postcalving population
Yield curve	Mortality and harvest	Depicts theoretical yield available from current prey as a function of Current Prey density relative to carrying capacity (Fig 16)

Model Parameters

Fixed model parameters control outputs of most model functions. Calculation of predation rates, predator functional responses, weather effects on natural mortality, differential prey vulnerability, harvest, wolf numerical responses, and density-dependent production and mortality are all controlled by model parameters.

Predation rates by wolves are based on mean pack size of the simulated wolf population. Ballard et al. (1987) described the relationship, $Y = 13.84\text{-}3.22 \cdot \ln X$ (Fig 17), where Y = adjusted days/kill and X = wolf pack size for 8 wolf packs from Alaska and Canada. Adjusted days/kill refers to conversion of kill rates for all prey species to the equivalent kill rate of 1 adult moose.

Converting biomass of all wolf prey items to adult moose equivalents allows general use of this function for all prey species in multi-prey systems. However, as noted before, consumption rates (kg/wolf/day) vary according to the primary prey species of the system. Calculation of rates determined solely by the theoretical consumption of adult moose equivalents results in daily consumption rates that overestimate those observed in many wolf-deer prey systems and in systems with low ungulate densities.

By adding an additional variable (Z) to Ballard's et al. (1987) equation, we allow users to simulate kill rates that result in consumption rates empirically derived from their own predator-prey system. The consumption rates resulting from the modified equation, $Y = Z(13.84\text{-}3.22 \ln X)$, are depicted in the Consumption Rate Chart (Fig 12) and listed in the Predator Vital Statistic Table (Fig 9). With those references the user can crosscheck and adjust output consumption rates (and, thereby, kill rates) to simulate empirical data. The consumption rate correction variable (Z) is entered as a Kill Factor, taking a value from zero to 1, in the Initial Model Variables dialog box. The effect of changing the consumption rate coefficient (Z) is illustrated in Figure 12.

Rarely, if ever, have predators caused the extirpation of their prey in large carnivore-ungulate, predator-prey systems. Examples of 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 is mediated by numerical and functional responses of predator populations to changes in prey abundance. Because the numerical response of predators often lags behind the decline in ungulates, a change in the per predator kill rate must occur to avoid extirpation of the prey. The conceptual basis for wolf-ungulate functional responses was summarized by Seip (1995) and Messier (1995). However, other studies failed to show a clear functional response by wolves to changing prey densities, possibly because of rapid numerical responses (Dale et al. 1995).

The Predprey functional response is incorporated into predation calculations for wolves, grizzly bears, and optional predators. The functional response equation was derived by simulating predator-caused population declines in moose and deer. 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 equation to generate a general type II functional response coefficient (FRC): $Y = -2.5x^2+4.3x-0.86$, where Y = the FRC, and X = the ratio of current prey biomass, a low density functional response threshold. Kill Rates are multiplied by the FRC to generate a functional response curve that is depicted in the Prey Density versus Kill Rate chart (Fig 13).

The FRC is dependent upon a user entry of a functional response threshold. The threshold value, which can be changed by the user, exists as a default value of 122,000 kg/1000 km^2, a biomass roughly equivalent to a moose density of 350 moose/1000 km^2 (0.9 moose/mi^2). When the current prey biomass falls below the threshold value, kill rates exhibit a $Y = -2.5x^2+4.3x-0.86$ functional response. Therefore, the user can change the steepness of the functional response curve by changing the threshold value. At values above the threshold value, the functional response coefficient is fixed at 1, creating a plateau in the functional response curve, i.e., the kill rate is constant. If the user selects a functional response threshold value of zero, the functional response coefficient defaults to 1, eliminating any functional response from the simulation.

Keith (1983) reviewed the relationship between wolf population growth rates and ungulate biomass among 7 North American wolf-ungulate systems. We added to that data set and derived a logarithmic function to simulate maximum potential growth rates for wolf populations in the presence of varying levels of ungulate biomass (Fig 18).

During each harvest year cycle within Predprey, wolf harvest is subtracted from the autumn wolf population to estimate the late winter population. Predicted wolf population growth is then calculated by the growth function (Fig 18) using an estimated mean winter population of $(W_a+W_w)/2$ where W_a is the autumn wolf population and W_w is the late winter population. The predicted increment is then added to the late winter population, simulating pup production and summer survival. Immigration and emigration are assumed equal.

Although ungulate biomass within a given predator-prey system may remain relatively constant over a period of years, the availability of that biomass to wolves is a function of prey vulnerability. Deep snow increases the vulnerability of ungulate prey to wolf predation (Gasaway et al. 1983; Peterson et al. 1984; Adams et al. 1995; Mech et al. 1995; Boertje et al. 1996), and wolf populations may exhibit a rapid numerical response to the increased availability of vulnerable prey following deep snow winters (Adams et al. 1995; Boertje et al. 1996). Predprey incorporates this increased wolf numerical response by randomly adding an additional 4% to 10% to the predicted wolf population growth following simulated severe winters. This stochastic parameter operates independent of the user's selection of stochastic or deterministic weather.

Help Menu

Work during the final reporting period of this project will primarily focus on completing the on-line help menu. To complete the help manual, the original draft will be expanded to include new model functions. Cell addresses that referred to the Lotus®1-2-3 for DOS® prototype must be changed to reflect the different cell addresses used in the Microsoft®Excel for Windows®95 version. Figure 19 illustrates the help menu outline.

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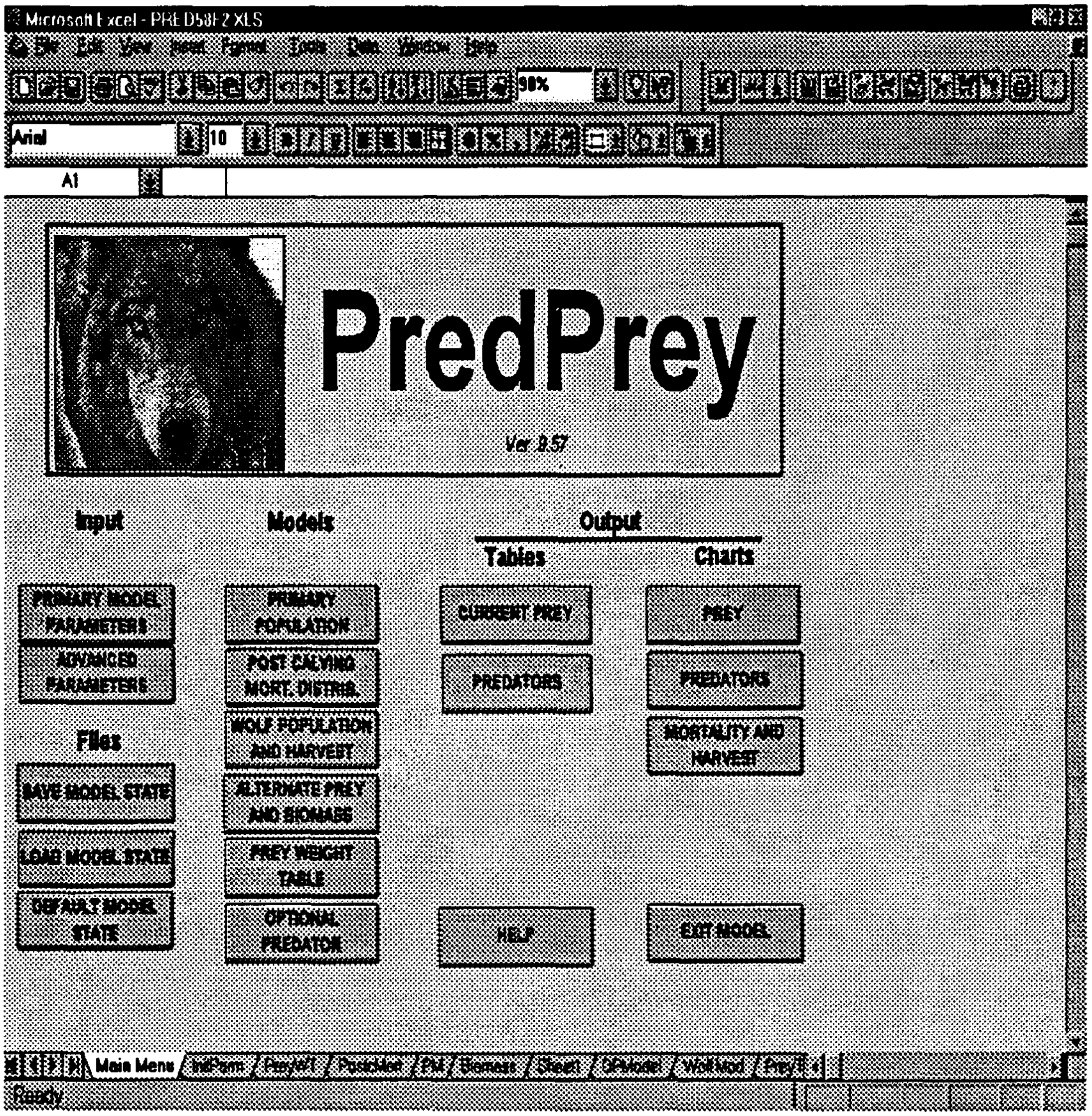


Figure 1 Screen Print of Main Menu dialog box where the user first enters Predprey

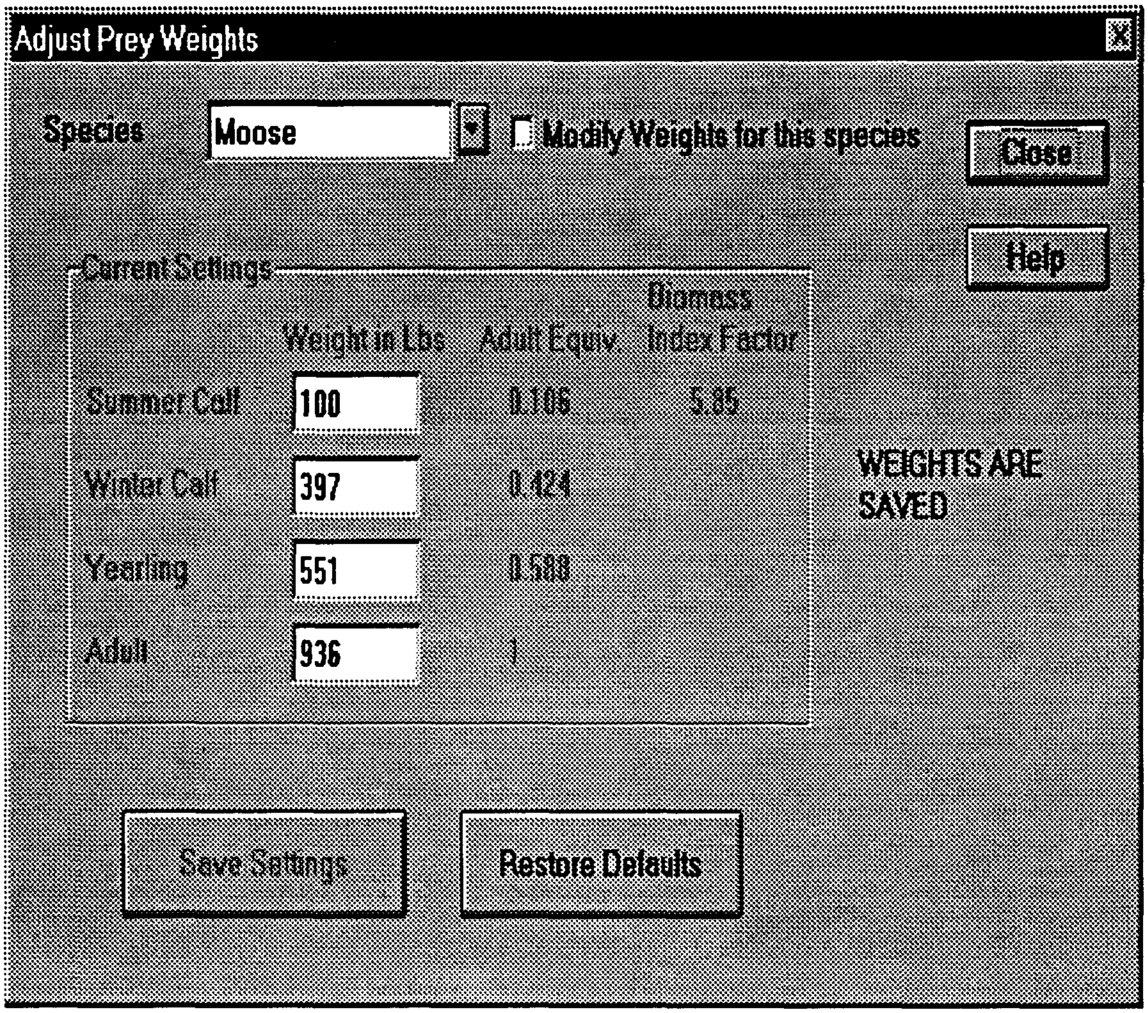


Figure 2 Prey Weight dialog box, allows user to customize physical characteristics of the simulated population

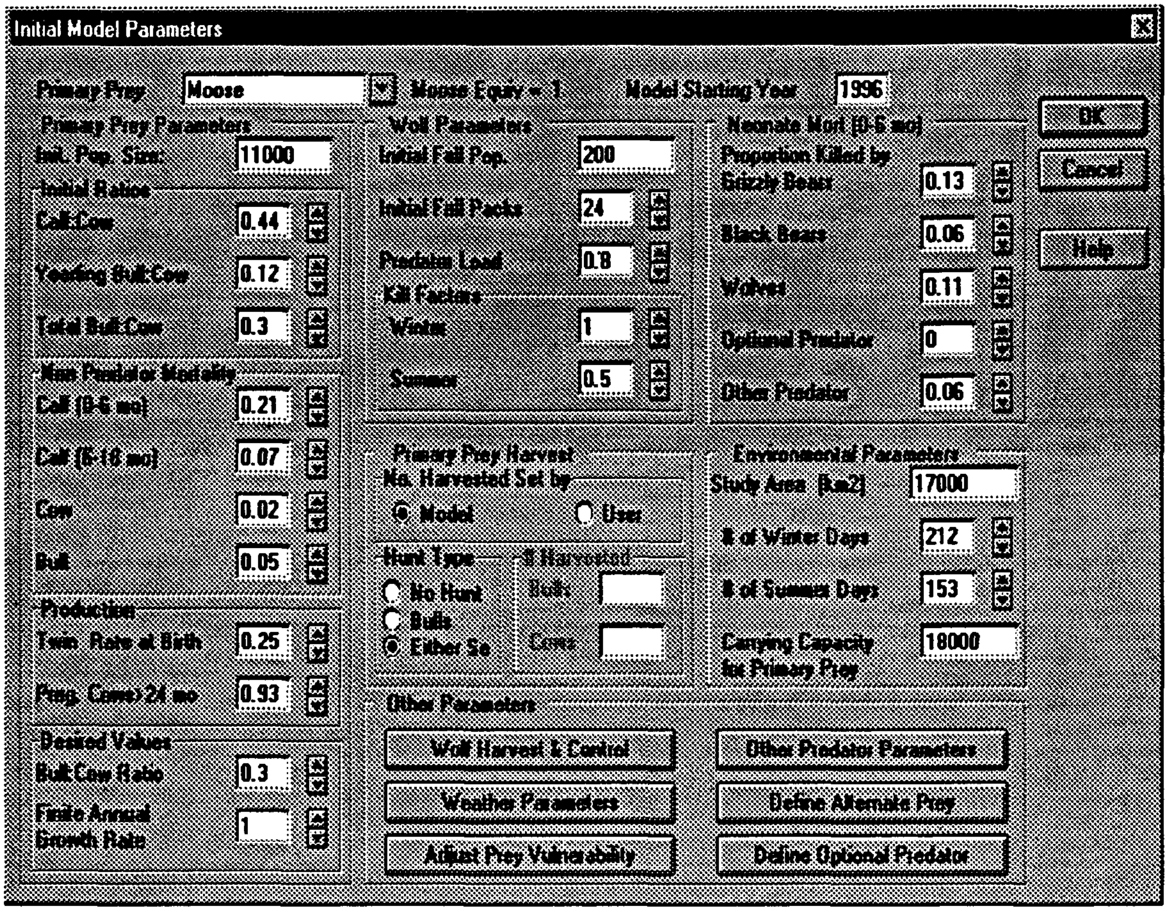


Figure 3 Initial Model Variables dialog box, used for entry of basic simulation characteristics

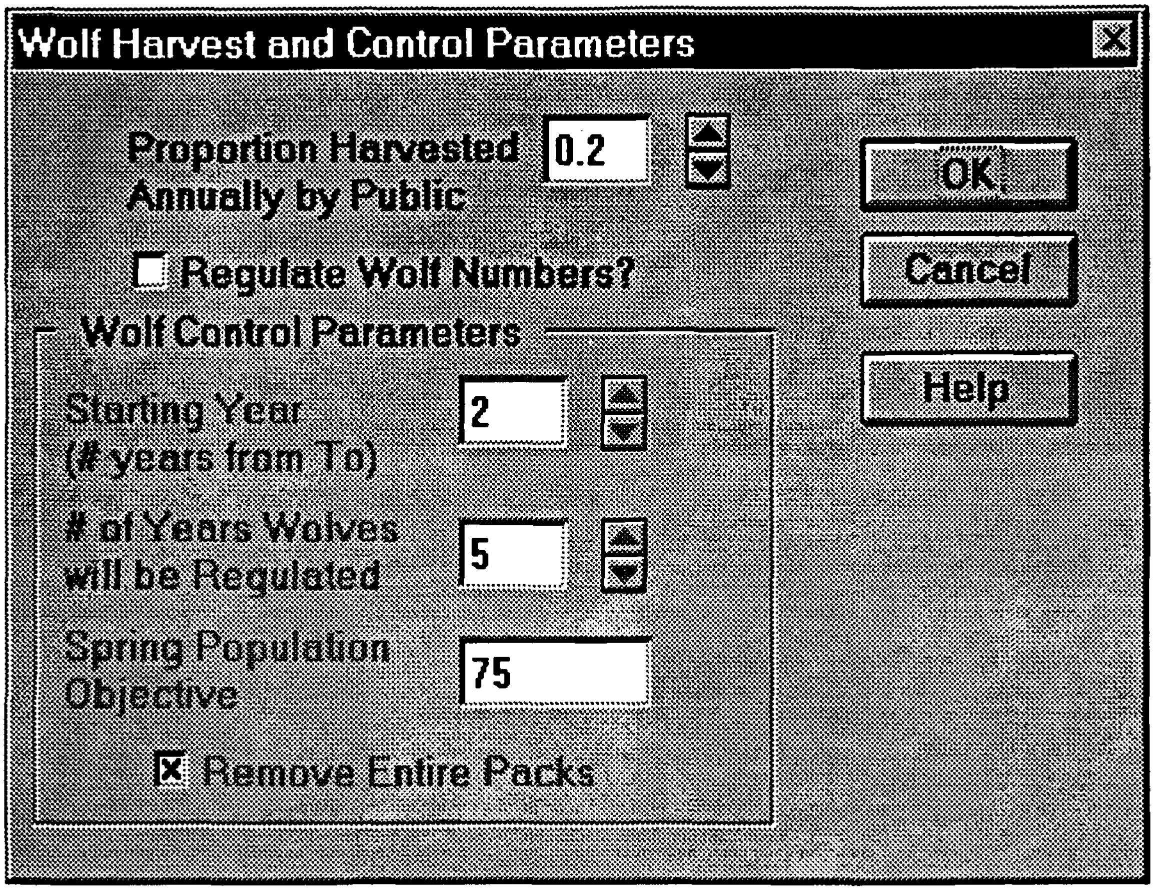


Figure 4 Wolf Harvest and Control Variables dialog box, allows entry of wolf harvest and prescription of wolf control programs

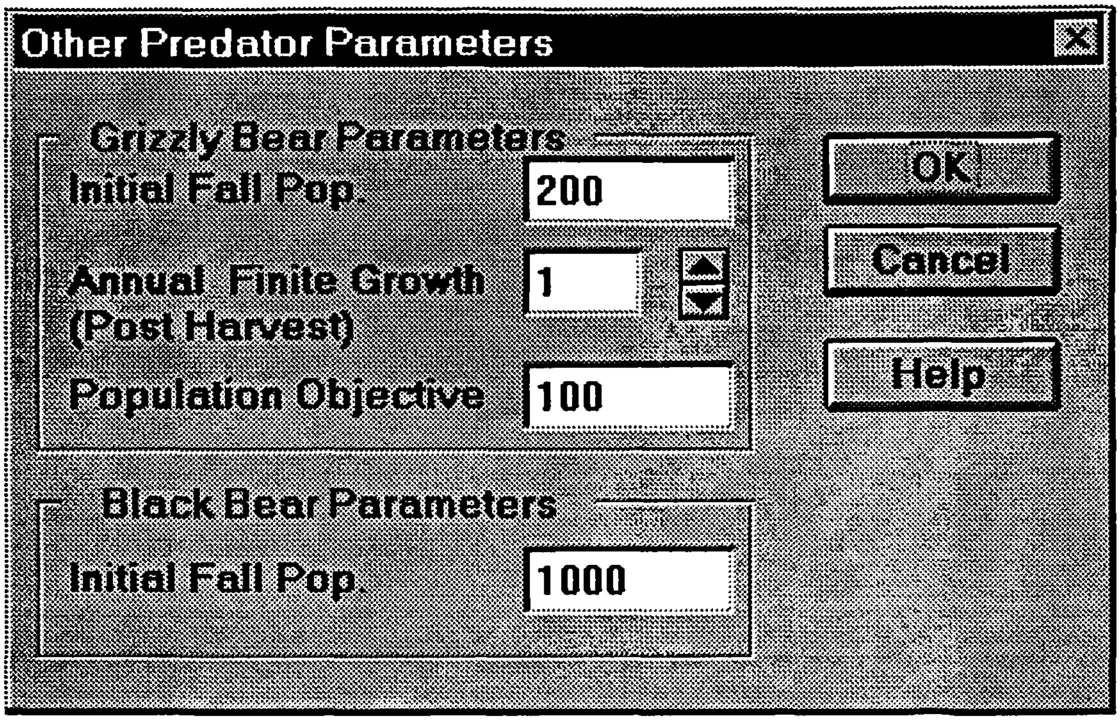


Figure 5 Bear Variables dialog box, finite growth rate defaults to 1.0 when objective is reached

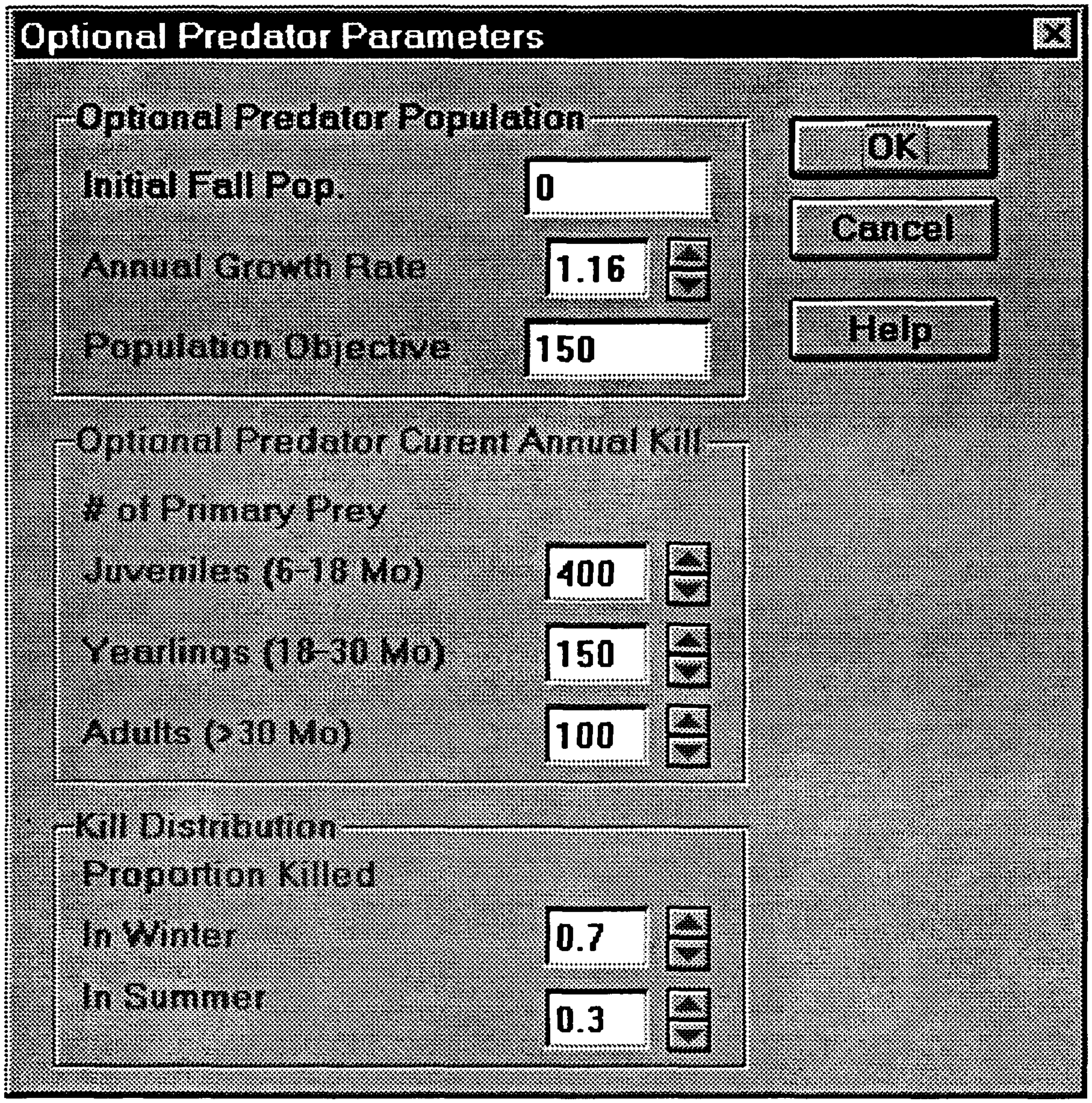


Figure 6 Optional Predator Variable dialog box, used to define population and predation characteristics of an optional predator

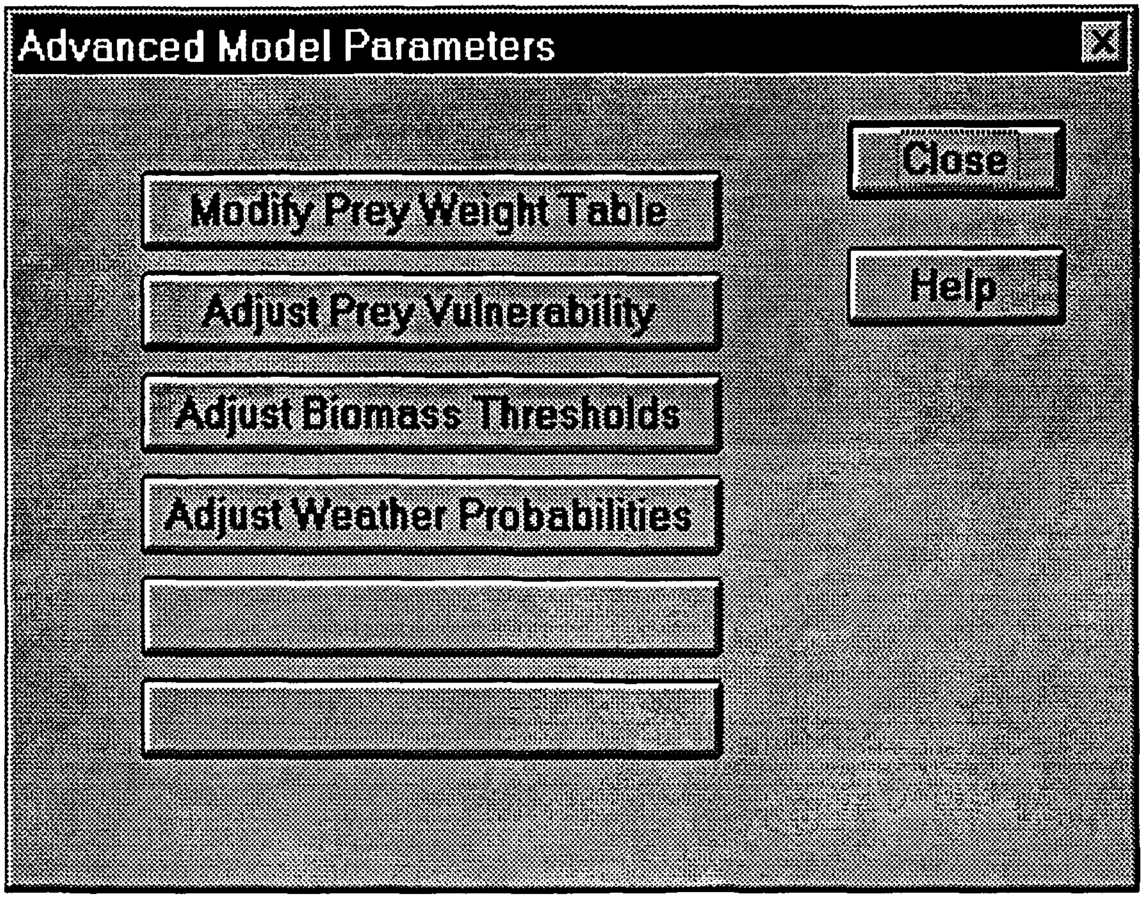
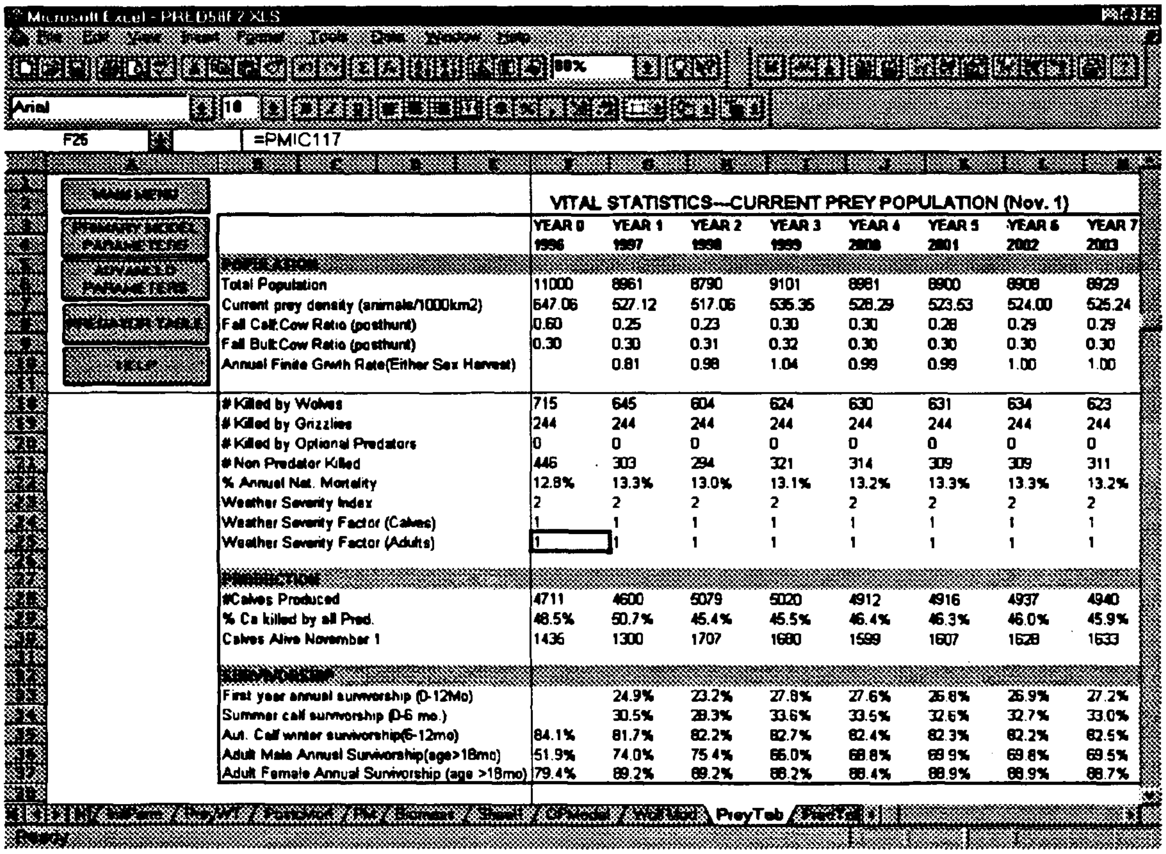


Figure 7 Advanced Model Variables dialog box, push buttons allow access to additional parameters



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VITAL STATISTICS---CURRENT PREY POPULATION (Nov. 1)

	YEAR 0 1996	YEAR 1 1997	YEAR 2 1998	YEAR 3 1999	YEAR 4 2000	YEAR 5 2001	YEAR 6 2002	YEAR 7 2003
Total Population	11000	8961	8790	9101	8981	8900	8908	8929
Current prey density (animals/1000km2)	647.06	527.12	517.06	535.35	528.29	523.53	524.00	525.24
Fall Calf:Cow Ratio (posthunt)	0.60	0.25	0.23	0.30	0.30	0.28	0.29	0.29
Fall Bull:Cow Ratio (posthunt)	0.30	0.30	0.31	0.32	0.30	0.30	0.30	0.30
Annual Finite Grwth Rate(Either Sex Harvest)		0.81	0.98	1.04	0.99	0.99	1.00	1.00
# Killed by Wolves	715	645	604	624	630	631	634	623
# Killed by Grizzlies	244	244	244	244	244	244	244	244
# Killed by Optional Predators	0	0	0	0	0	0	0	0
# Non Predator Killed	446	303	294	321	314	309	309	311
% Annual Nat. Mortality	12.8%	13.3%	13.0%	13.1%	13.2%	13.3%	13.3%	13.2%
Weather Severity Index	2	2	2	2	2	2	2	2
Weather Severity Factor (Calves)	1	1	1	1	1	1	1	1
Weather Severity Factor (Adults)	1	1	1	1	1	1	1	1
#Calves Produced	4711	4600	5079	5020	4912	4916	4937	4940
% Ca killed by all Pred.	48.5%	50.7%	45.4%	45.5%	46.4%	46.3%	46.0%	45.9%
Calves Alive November 1	1436	1300	1707	1680	1599	1607	1628	1633
First year annual survivorship (0-12Mo)		24.9%	23.2%	27.8%	27.6%	26.8%	26.9%	27.2%
Summer calf survivorship (0-6 mo.)		30.5%	28.3%	33.6%	33.5%	32.6%	32.7%	33.0%
Aut. Calf winter survivorship(6-12mo)	84.1%	81.7%	82.2%	82.7%	82.4%	82.3%	82.2%	82.5%
Adult Male Annual Survivorship(age>18mo)	51.9%	74.0%	75.4%	66.0%	68.8%	69.9%	69.8%	69.5%
Adult Female Annual Survivorship (age >18mo)	79.4%	89.2%	89.2%	88.2%	88.4%	88.9%	88.9%	88.7%

Figure 8 Screen print of Prey Vital Statistic Table lists commonly used population statistics for current prey species

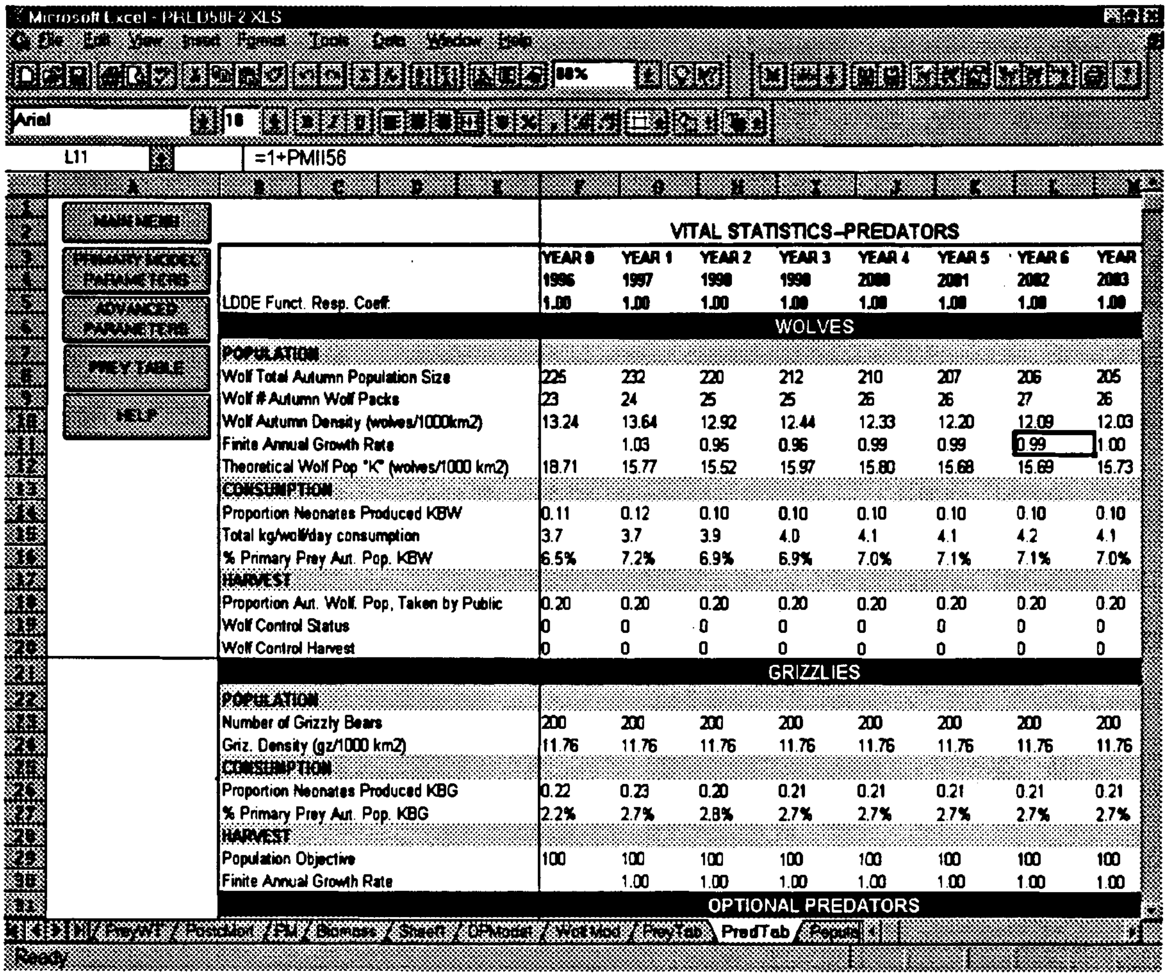


Figure 9 Screen print of Predator Vital Statistics Tables lists commonly used statistics for all predators

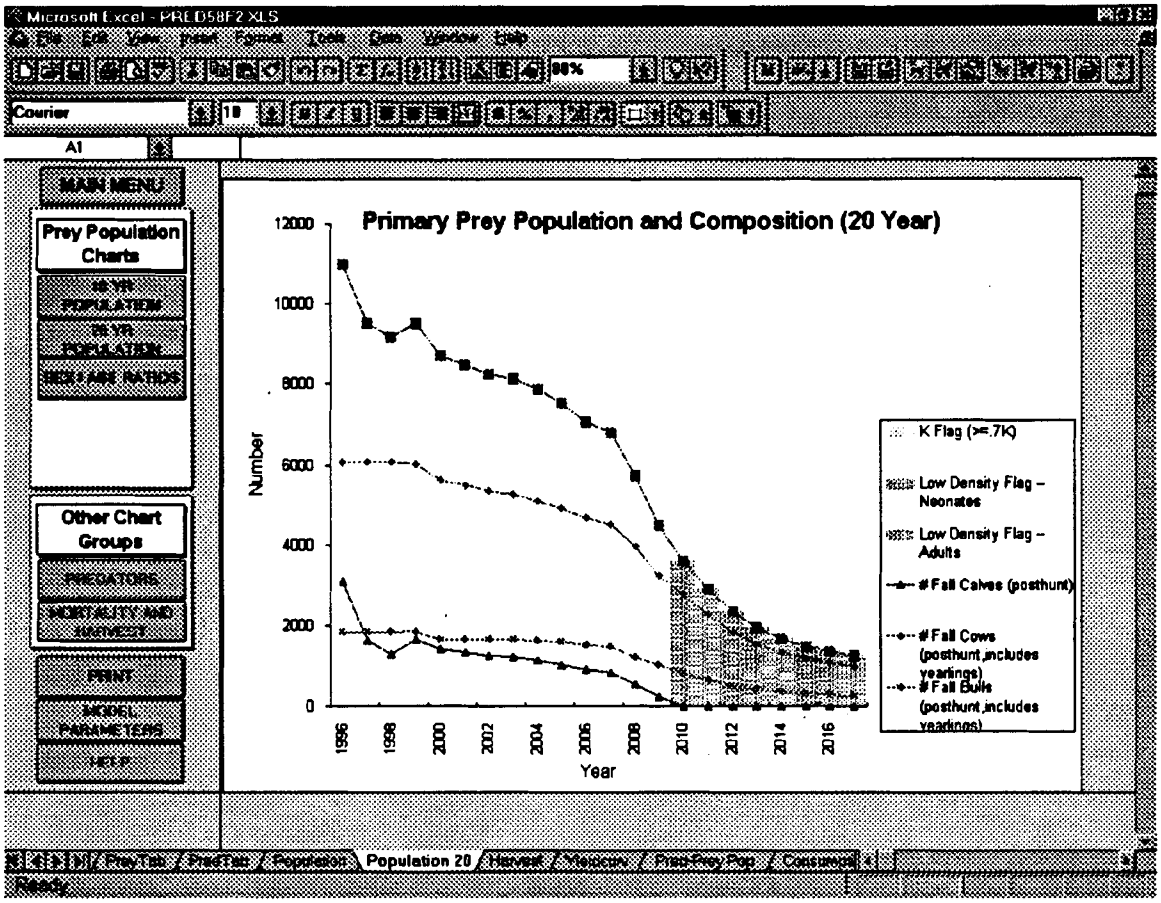


Figure 10 Screen print of 20-year Primary Prey chart depicting changes in total prey population and in different sex and age classes

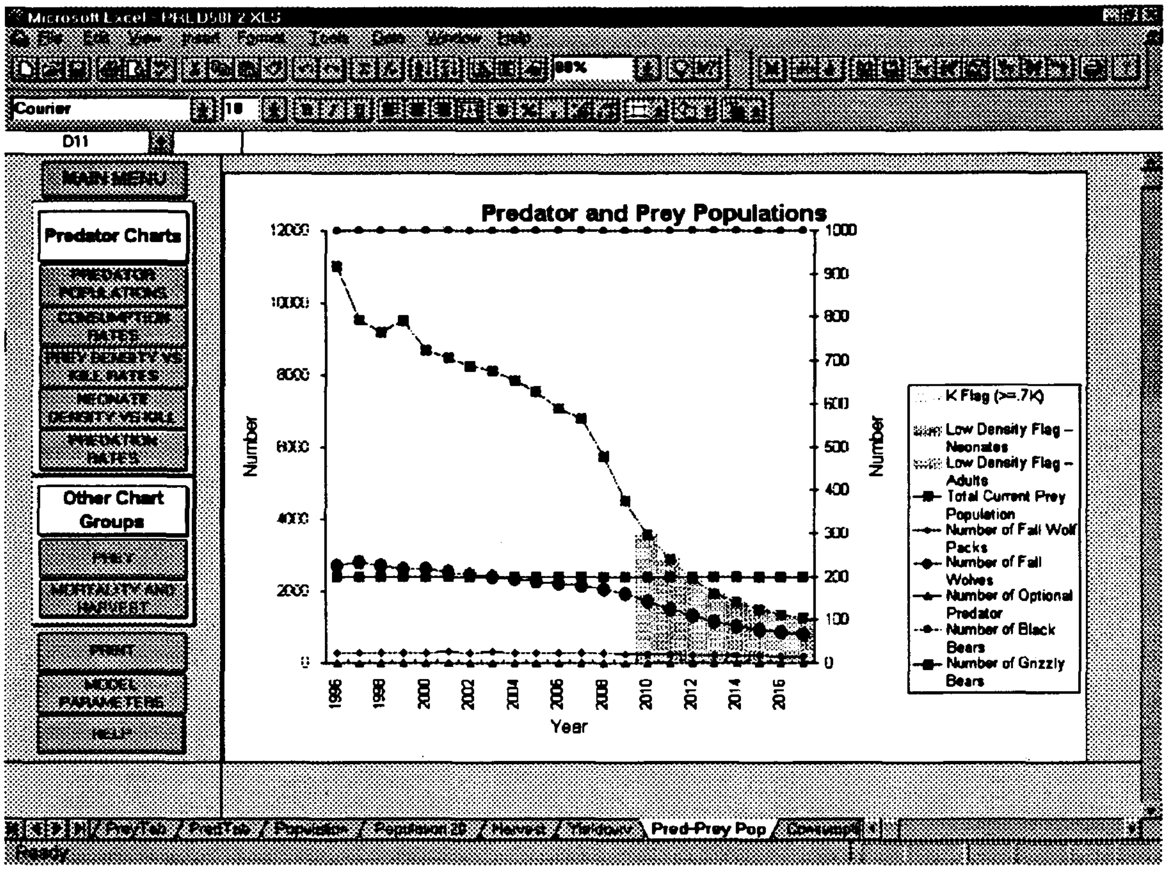
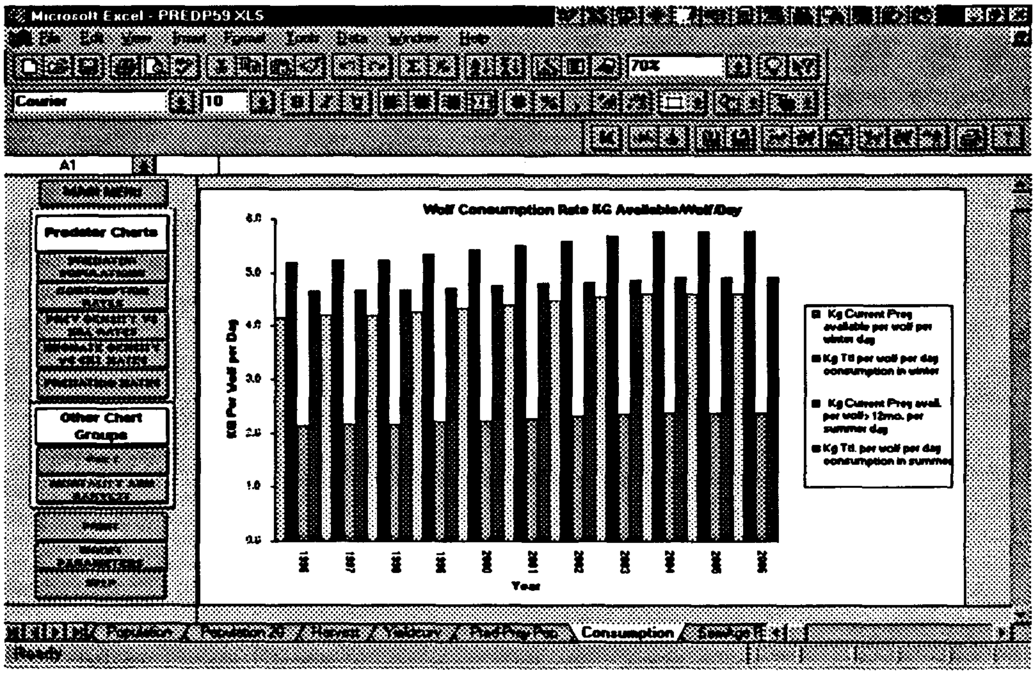


Figure 11 Screen print of 20-year Predator Chart comparing changes in predator populations with that of current prey. Note: wolf numerical response time lag, 1996-2000



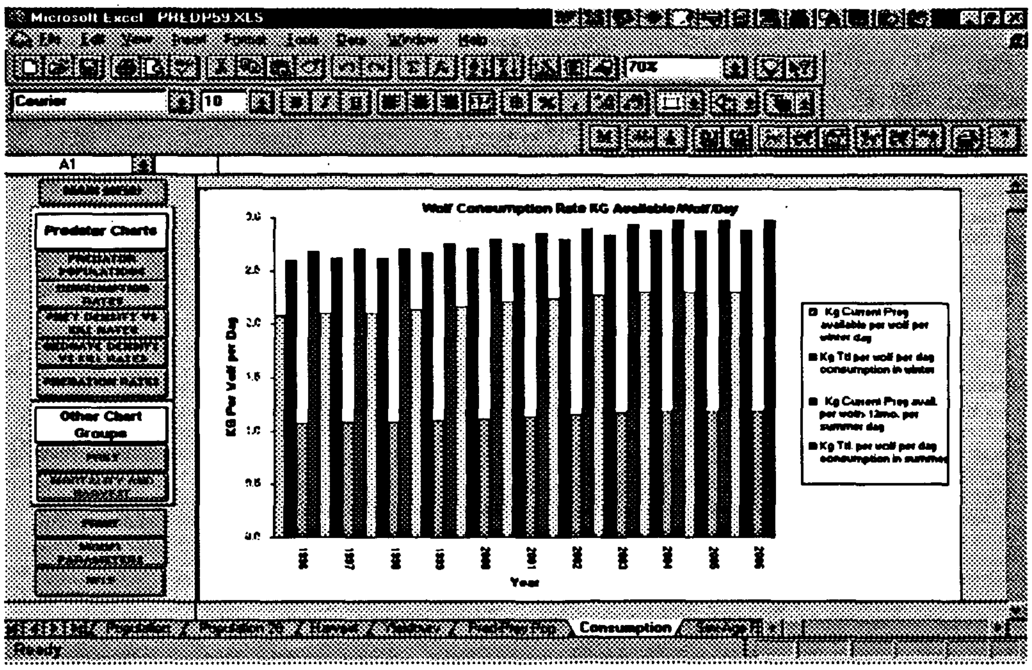


Figure 12 Screen prints of Consumption Rate charts. Illustrates how changes in kill rate variable in Initial Variables dialog box can be used to adjust consumption rates to fit empirical rates. Top chart consumption rates average 5.5 kg/wolf/per day, Kill Rate variable set at 1.0; Bottom chart consumption rates average about 2.75 kg/wolf/day, Kill Rate variable set at 0.5.

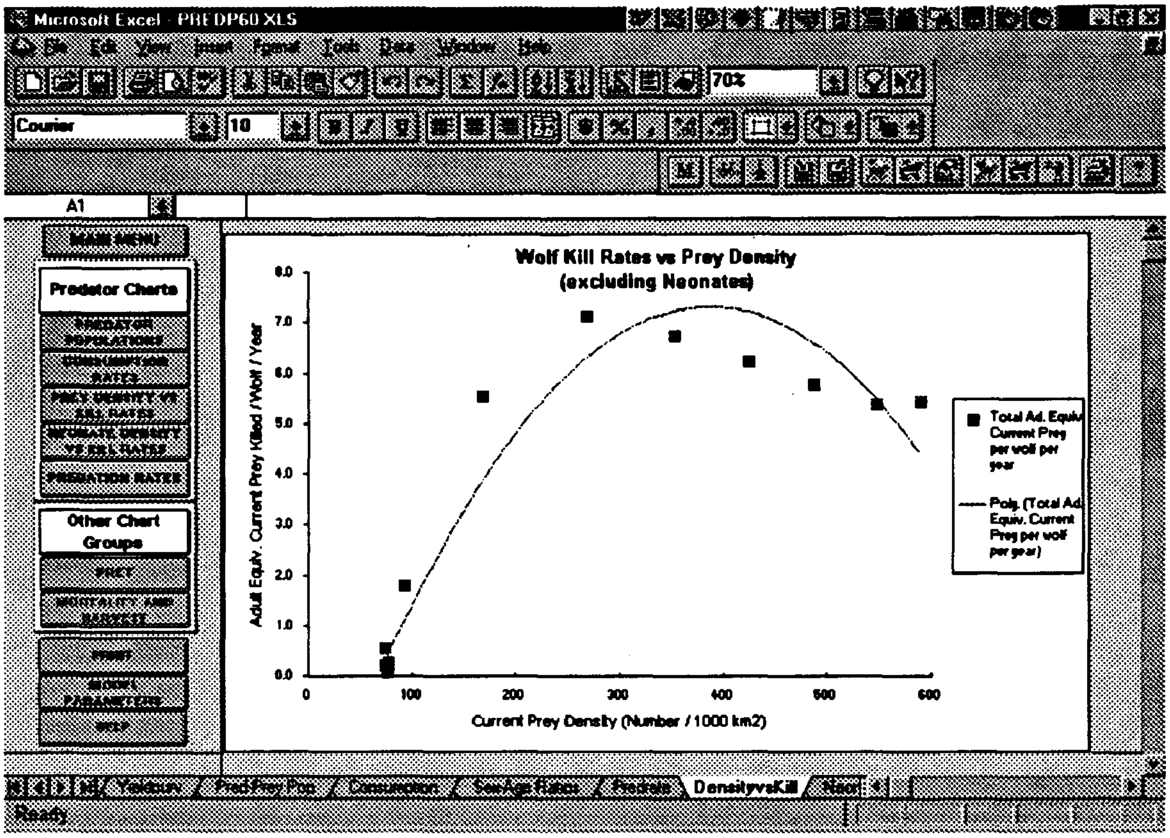


Figure 13 Screen print of Prey Density versus Kill Rate chart compares predation with changes in prey density. Current version uses second order polynomials to fit line to data (curved line). Final version will use logarithmic or third order polynomial to improve fit.

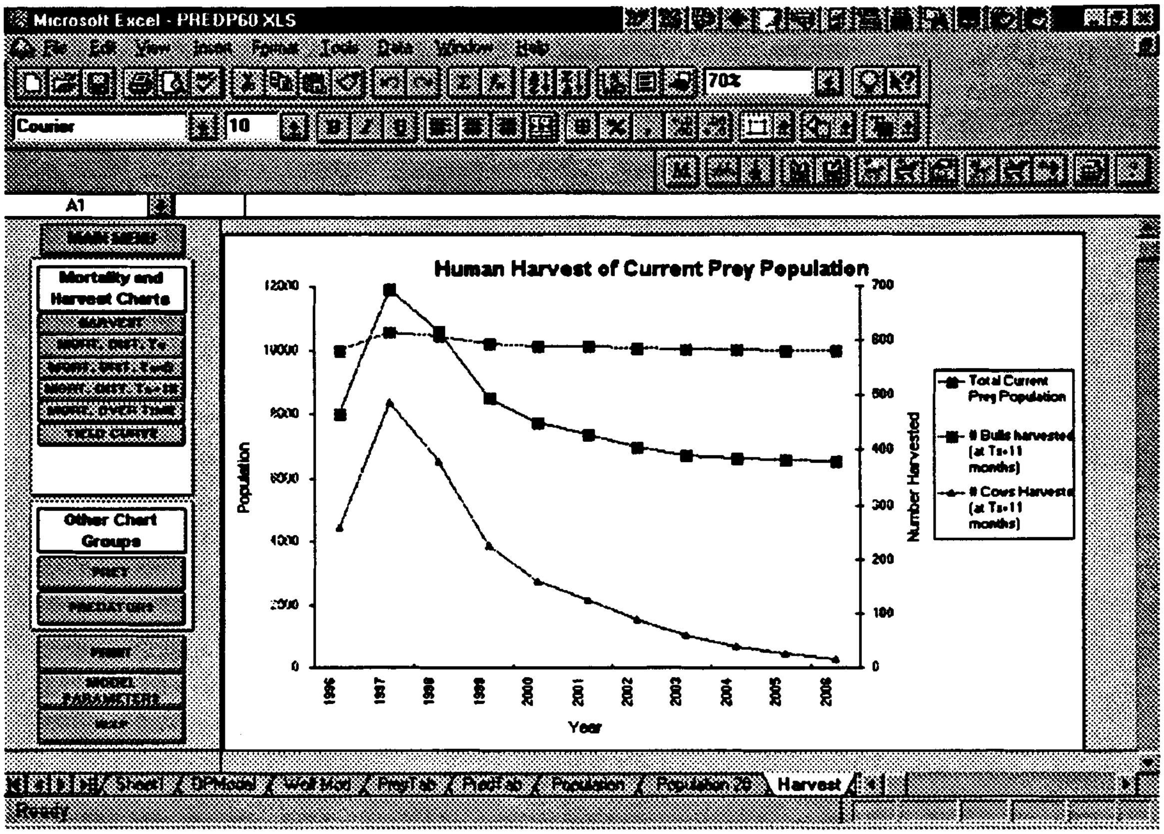


Figure 14 Screen print of Harvest chart showing model population response in the presence of slowly increasing wolf population. Harvest was generated by model to meet user- specified population growth rates and bull:cow ratios in the presence of predation by wolves and bears. Harvest scale on right y axis, total population scale on left y axis.

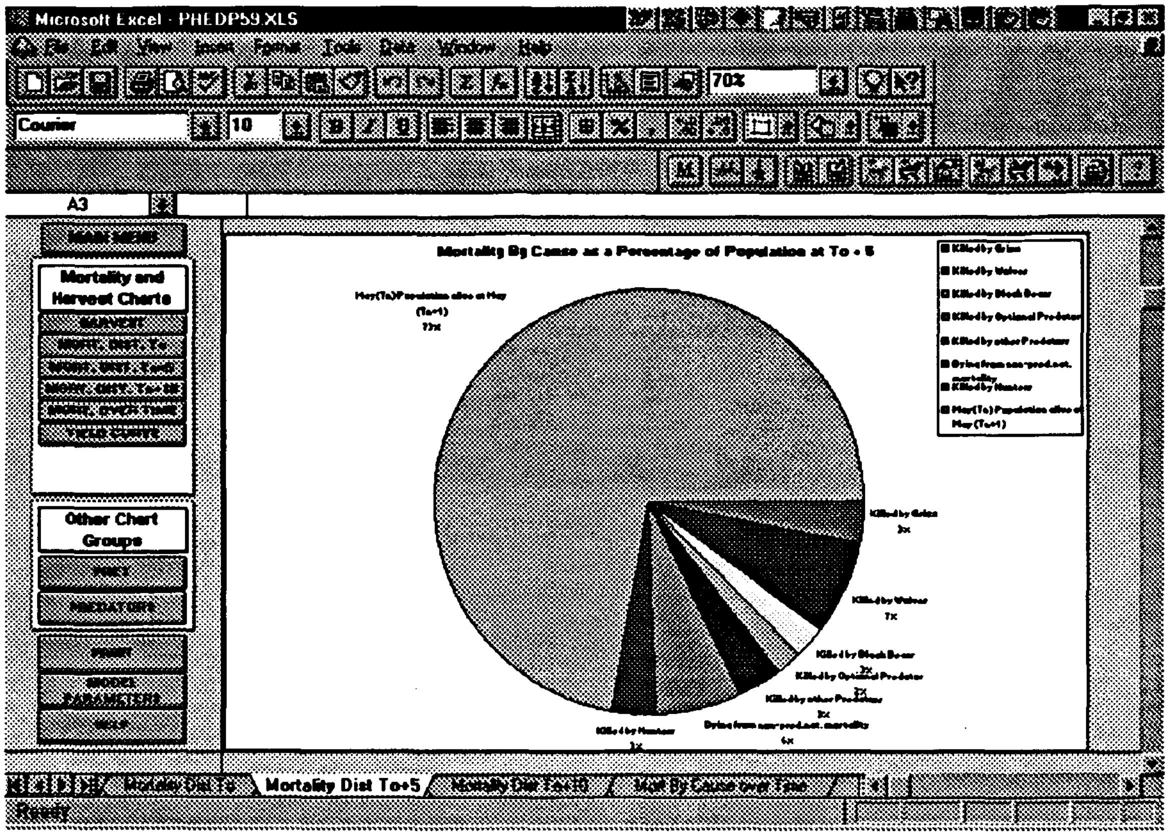


Figure 15 Screen print of Mortality Distribution pie chart of the current prey population for the biological year population beginning 1 May in year T and ending 30 April in year T+1

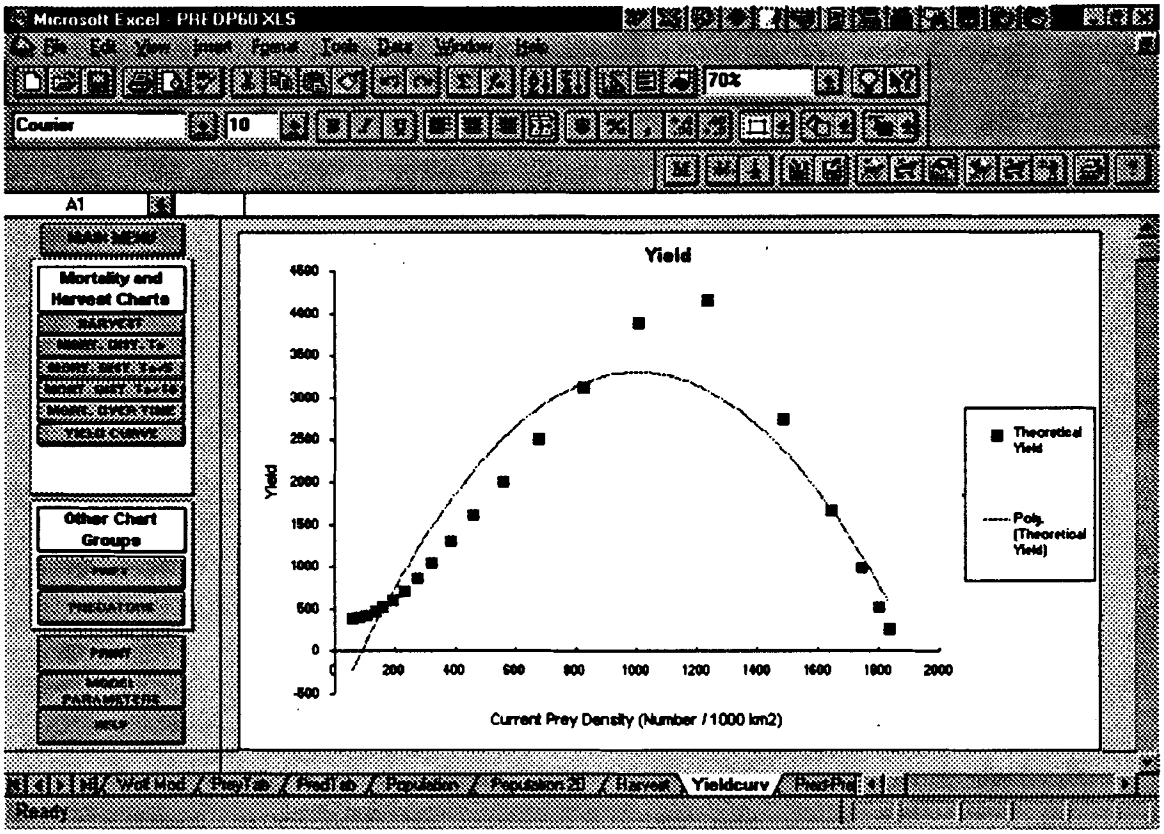


Figure 16 Screen print of Yield Curve. Depicts theotretical yield from simulated population in the absence of predators and in the presence of density-dependent effects. Current version of Predprey uses second order polynomial (curved line) to fit data points. Final version will use third order polynomial for improved fit. Note: skewed peak of yield to left of midpoint.

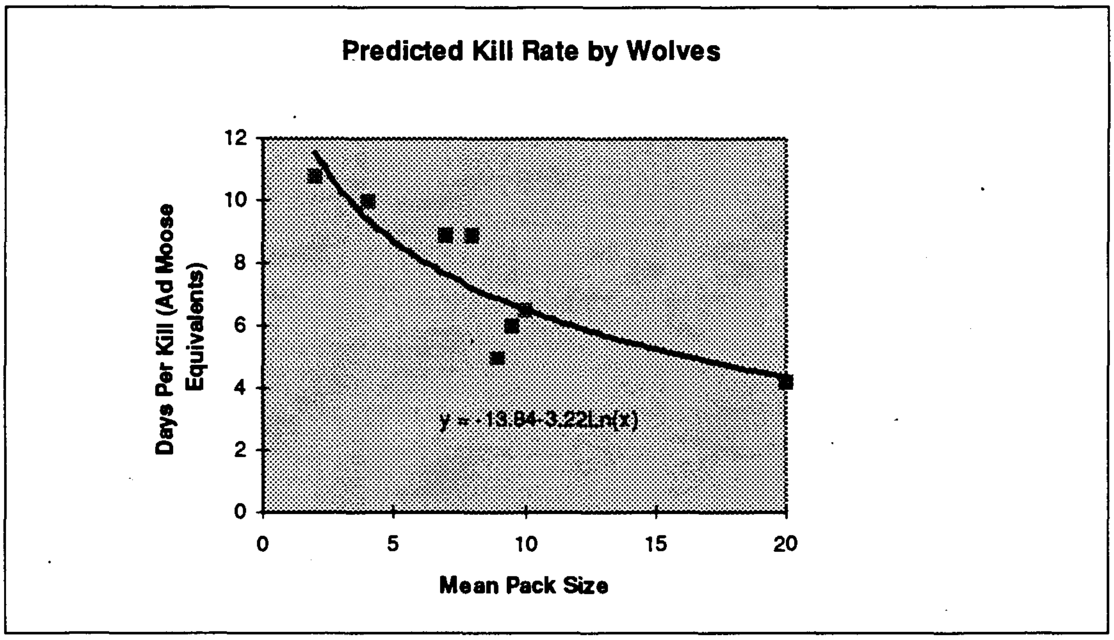


Figure 17 Original wolf predation function used in Predprey to predict kill rates by wolves at various mean pack sizes (from Ballard 1987). Current version of Predprey uses slight modification of this basic function. The modification incorporates a kill factor coeffecient (z) to allow user to adjust consumption rates to match empirical values.

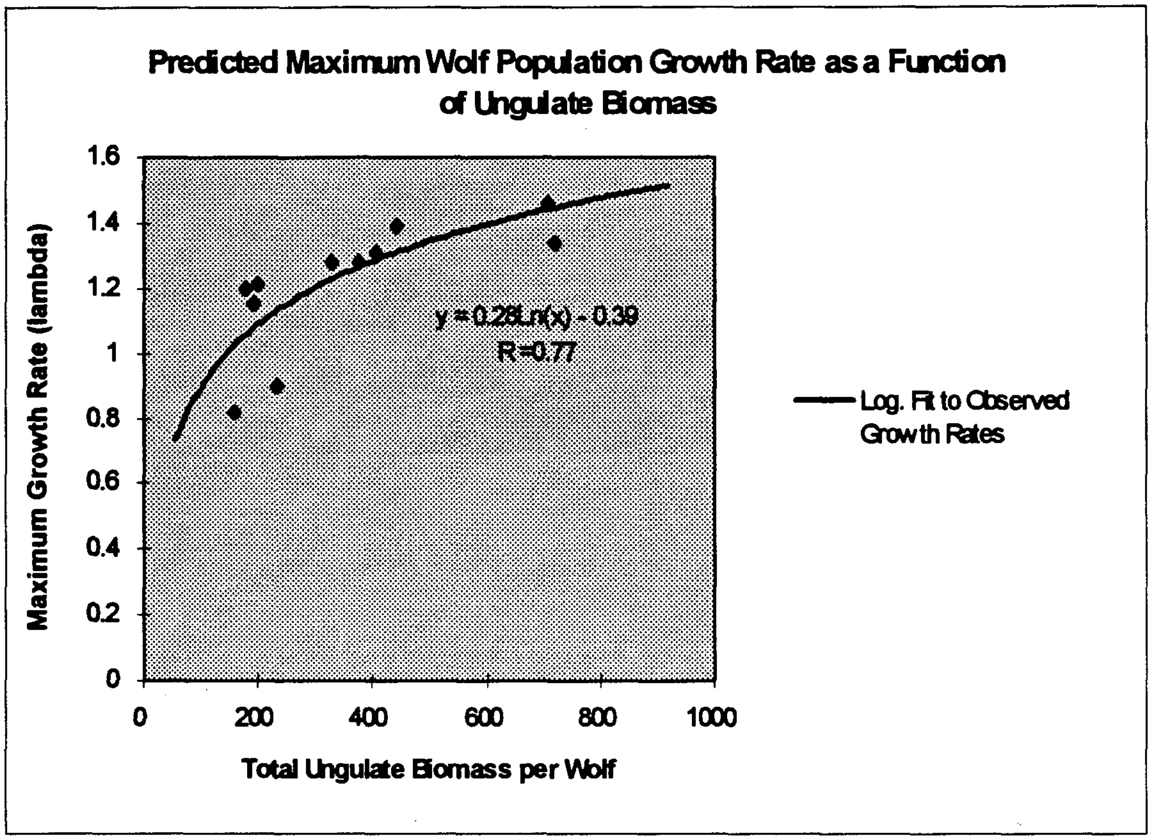


Figure 18 Predprey wolf population growth parameter derived to predict wolf population numerical response to changes in ungulate biomass (modified from Keith 1983). Note: function yields negative wolf population growth rates (i.e., $\lambda < 1.0$) at low ungulate biomass values.

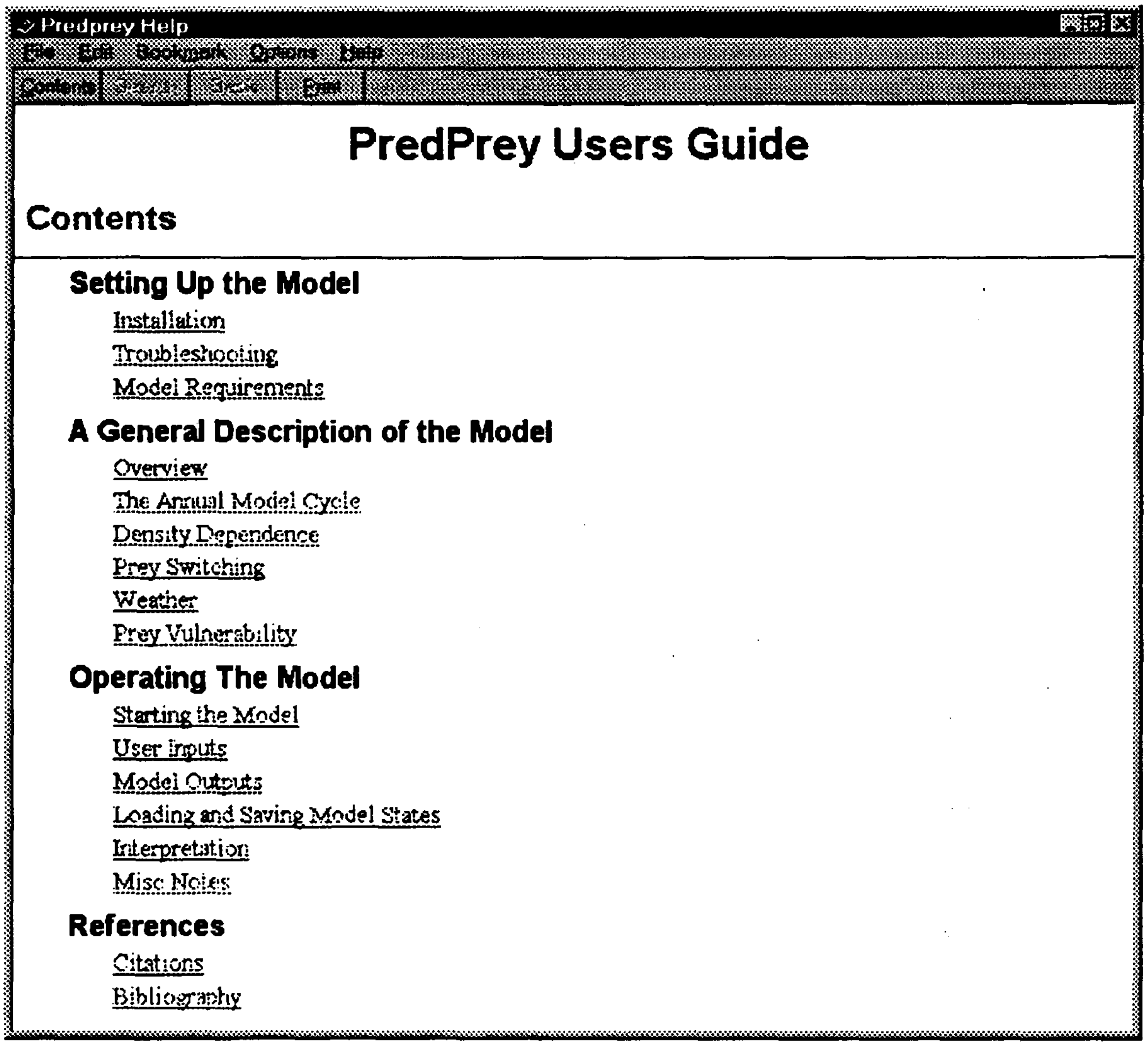
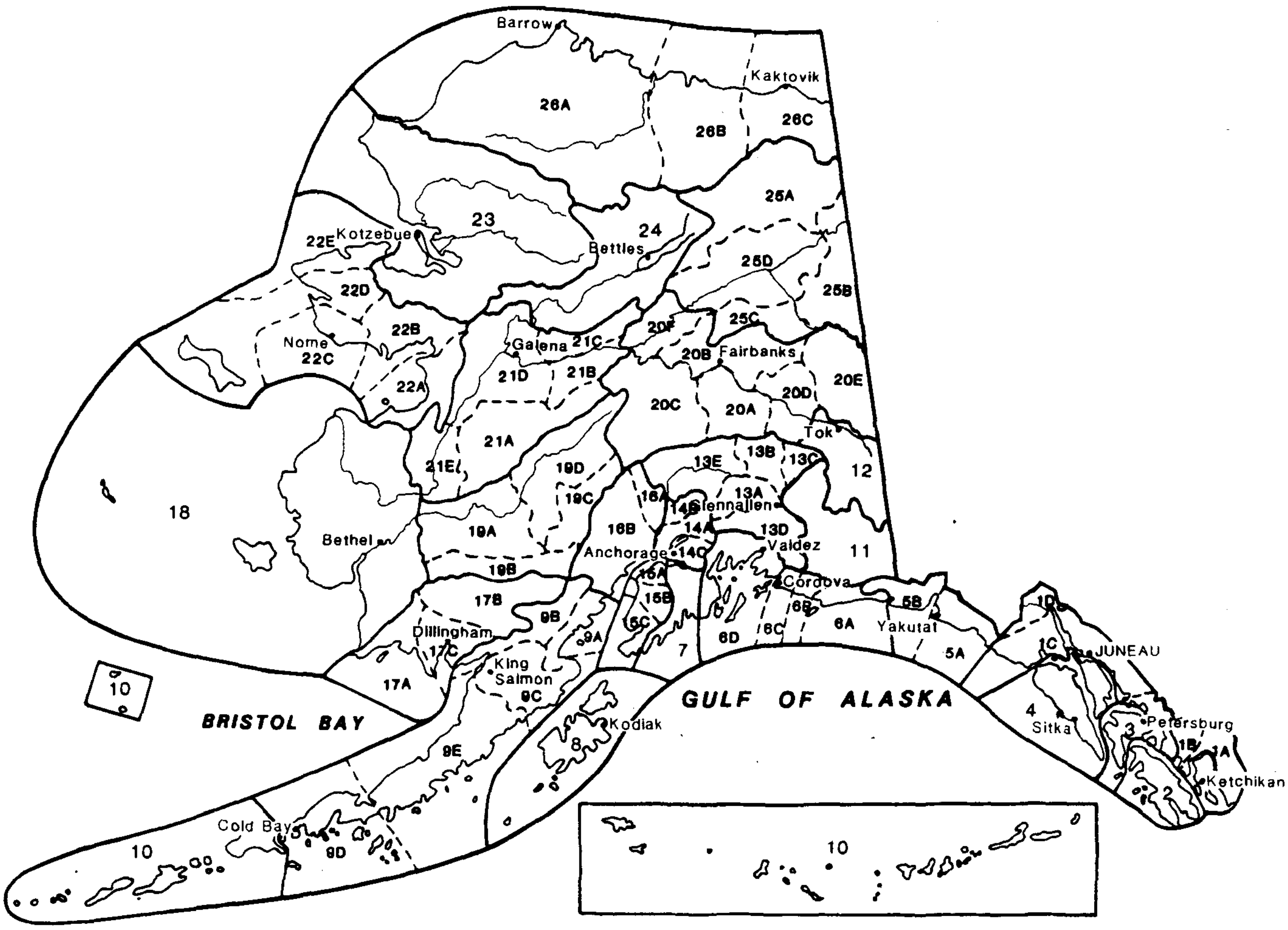


Figure 19 Screen print of preliminary help menu outline

Alaska's Game Management Units



The Federal Aid in Wildlife Restoration Program consists of funds from a 10% to 11% manufacturer's excise tax collected from the sales of handguns, sporting rifles, shotguns, ammunition, and archery equipment. The Federal Aid program allots funds back to states through a formula based on each state's geographic area and number of paid hunting license holders. Alaska receives a maximum 5% of revenues collected each year. The Alaska Department of Fish and Game uses federal aid funds to help restore, conserve, and manage wild birds and mammals to benefit the public. These funds are also used to educate hunters to develop the skills, knowledge, and attitudes for responsible hunting. Seventy-five percent of the funds for this report are from Federal Aid.