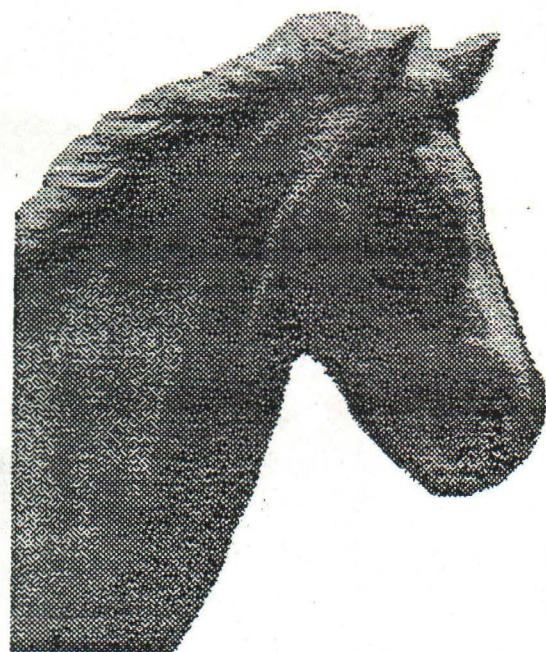


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WILD HORSE POPULATION MODEL

Version 2.1

USER'S GUIDE

Stephen H. Jenkins

Department of Biology
University of Nevada
Reno, Nevada 89557

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INTRODUCTION

This is a population model for wild horses, designed to help evaluate various management plans that might be considered for a particular area. The model uses data on survival and reproductive rates of horses to project population growth for up to 50 years. The model uses a random process to account for unpredictable future variation in these demographic parameters. This random process reflects the fact that future environmental conditions that may affect horse populations can't be known in advance. Therefore each trial with the model will give a different pattern of population growth -- some trials may include mostly "good" years, others may include a series of several "bad" years in succession. This **stochastic** approach to modeling population growth uses repeated trials to project a range of possible population sizes after a given number of years, which is more realistic than predicting a single, specific population size.

The model can be used to compare many different strategies of removal and fertility treatment. One important aspect of population dynamics that is **not** included in the present model is density-dependent mortality and reproduction in horses. There is some evidence that these processes are density-dependent, but there are insufficient data at this time to use in a model.

USE AND ABUSE OF POPULATION MODELING

Population modeling is widely used in ecology and conservation biology, but has several pitfalls that must be discussed. The most important of these is that results may be taken too seriously as **predictions** of what will happen to a particular population in the future. Caswell (1989) makes an important distinction between **forecasting** and **projection** as potential uses of a population model: "A forecast is an attempt to predict what *will* happen. A projection is an attempt to describe what *would* happen, given certain hypotheses" (Caswell 1989: 20). What you are really doing when you use the *Horse* model to project population growth is saying: **If** a set of assumptions about survival, reproduction, environmental variability, and management actions hold true, **then** we expect the population to grow at a certain rate determined by the model. In other words, the results of this model, like those of any model, depend on its assumptions, and the user must always keep those assumptions in mind when interpreting the results. Too often, once output is produced from a model, the assumptions tied to that output are forgotten in the user's enthusiasm for the apparent specificity and concreteness of the results.

Given this danger of taking results of the program too literally as forecasts of future population growth, what is the best use of the model? I think the most appropriate and effective way to use the model is for **comparison** of population growth under various conditions. The model is specifically designed for comparing fertility control and removal as management strategies. It can also be used to compare effects of different levels of environmental variability on population growth. I urge users to adopt an exploratory attitude when running the program. If you don't have all the necessary data for your population, make up some numbers and see what happens! The most important objective of the program is to help you learn more about population dynamics of wild horses, not to use it as a crutch to make management decisions for you.

INSTALLATION

Before installing the program on your hard disk, it would be wise to make a working copy of the installation diskette. To do so, format a blank diskette, then place the installation diskette in your 3½" disk drive and type the following at the DOS prompt:

```
diskcopy a: a:
```

or

```
diskcopy b: b:
```

depending on whether your 3½" drive is identified as *a:* or *b:* by your system. Follow the instructions to swap disks that appear on the screen. Label the working diskette, store the original installation diskette in a safe place, and use the working diskette to run the program or install it on your hard disk.

To install the *Horse* program and associated help and data files on your hard disk, place the working diskette in drive *a* and type:

```
a:\install
```

(or *b:\install* if you are using disk drive *b*). Follow the instructions that appear on the screen to complete the installation. View the **readme** file for additional notes on installation, including procedures to install the program for Microsoft Windows or run the program directly from the diskette.

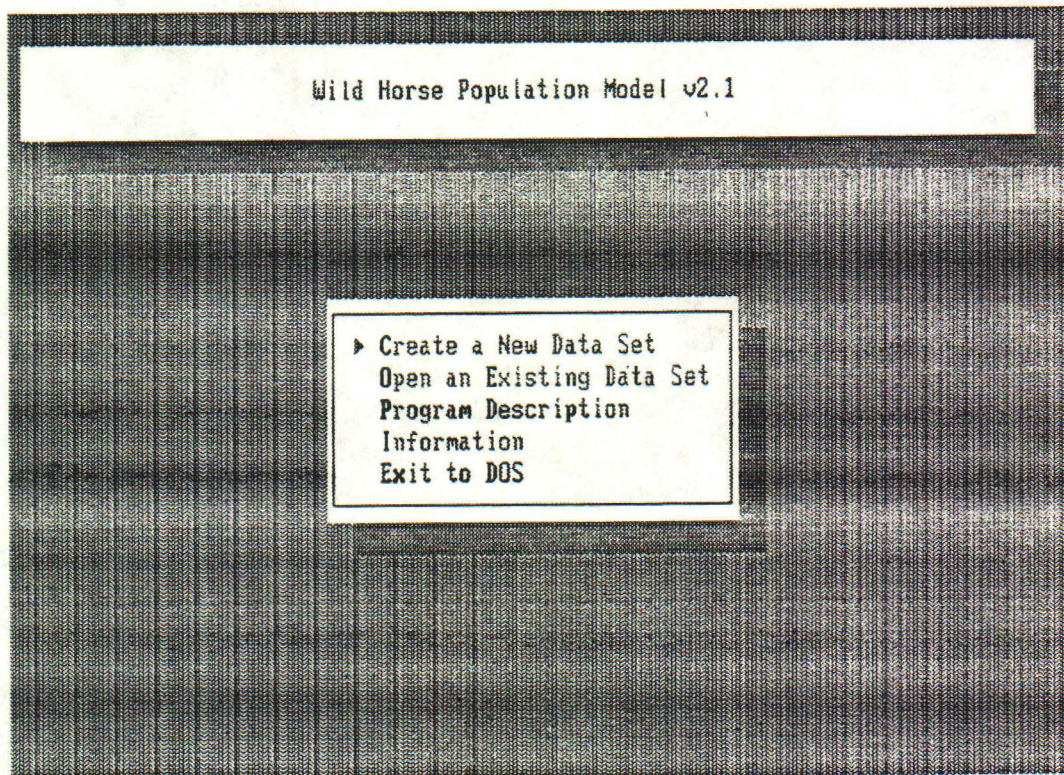
Once the program is installed on your hard disk, you must reboot your computer before running it for the first time. To run the program, type the following at any DOS prompt:

```
c:\horseshj\horse
```

TUTORIAL

All of your interaction with the program is through a series of menus in which you enter data or make choices about various options for management, form of output, etc. On-line help is available for each menu. Therefore, it should be relatively easy to learn how the program works just by running it. If you feel more comfortable going through this tutorial before you start playing with the program on your own, do so; otherwise use this tutorial only if you get stuck on a particular part of the program.

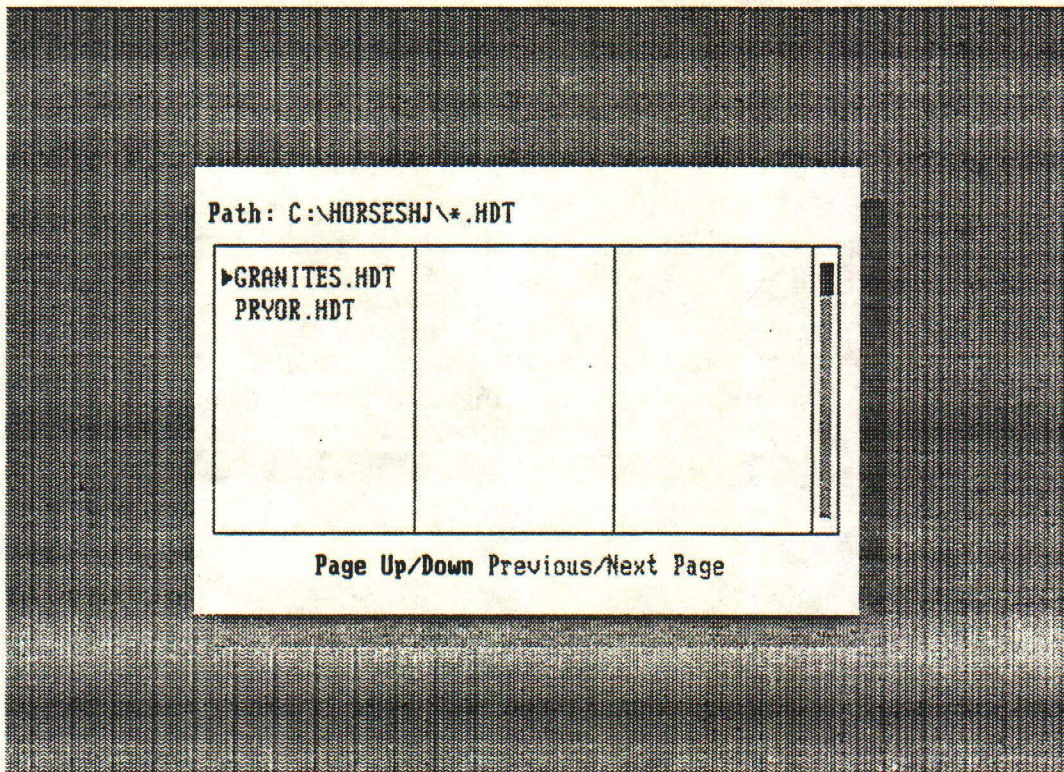
If you've installed the program successfully and started it running as described above, you will soon see a title screen. After about 3 seconds, this introductory menu will appear:



F1 Help | Esc Exit | Use arrows or press highlighted letter to select

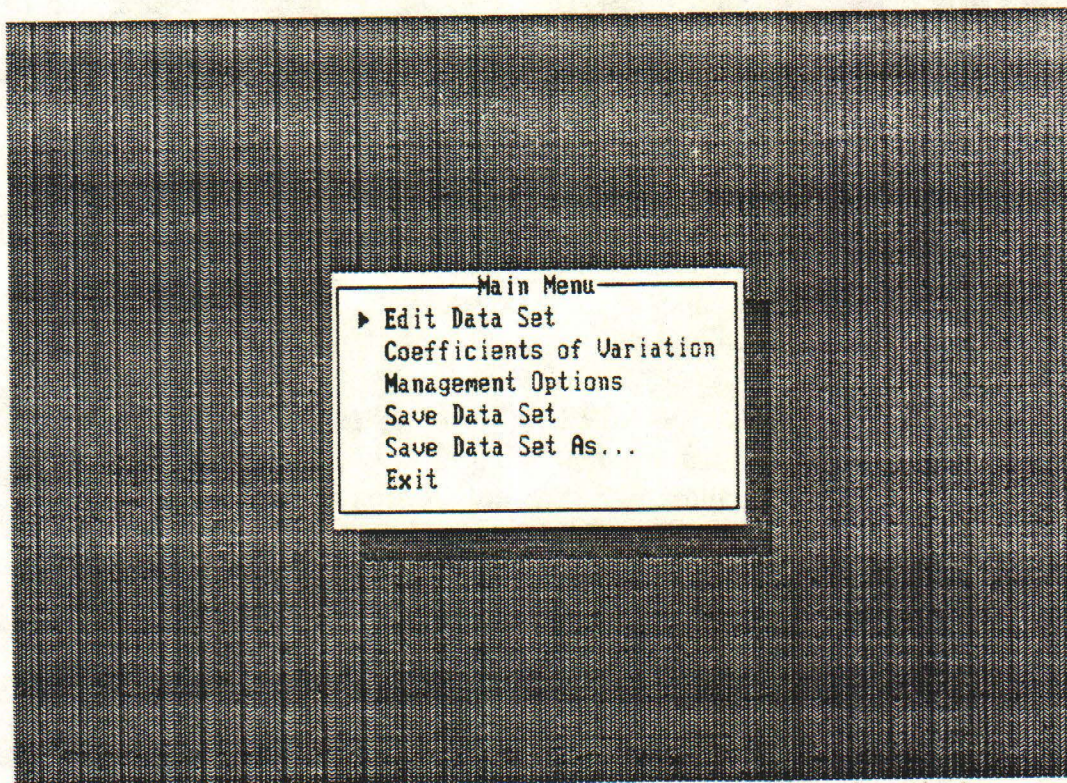
Notice the line at the bottom of the screen. This describes how to make choices from the menu and states what two important keys do. Function key F1 at the top or left hand side of your keyboard displays a context-sensitive help screen. The Escape key takes you back to the previous menu (in this case, since there is no previous menu, the Esc key stops the program and returns you to DOS).

To choose an item from the menu, type the highlighted letter, or use the arrow keys to move the pointer up or down and hit **Enter** when you are ready. Let's begin by typing **O** to *Open an Existing Data Set*. You should now see a file selection menu:



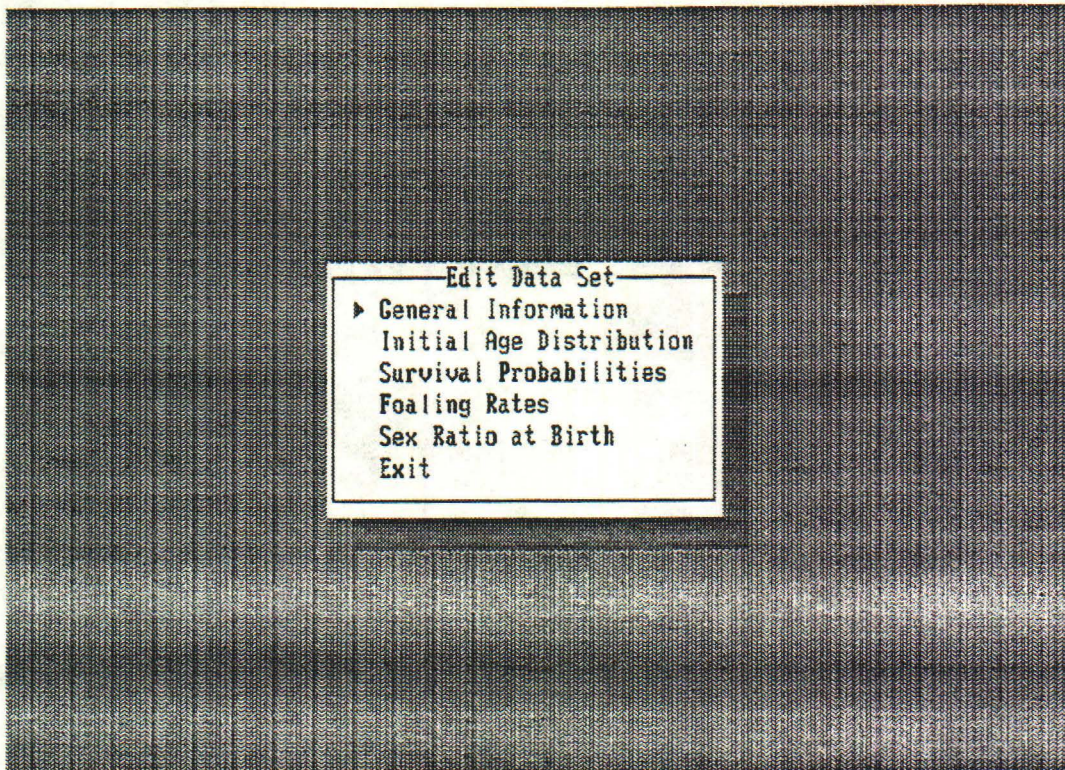
F1 Help | Use arrows or press highlighted letter to select

This box lists all of the data files supplied with the program, as well as new data files you may have created and stored in the C:\HORSESHJ directory. Use the ↓ key to move the pointer to the file named **PRYOR.HDT**, and hit **Enter** to select this file. Now you will see the Main Menu, as reproduced below:



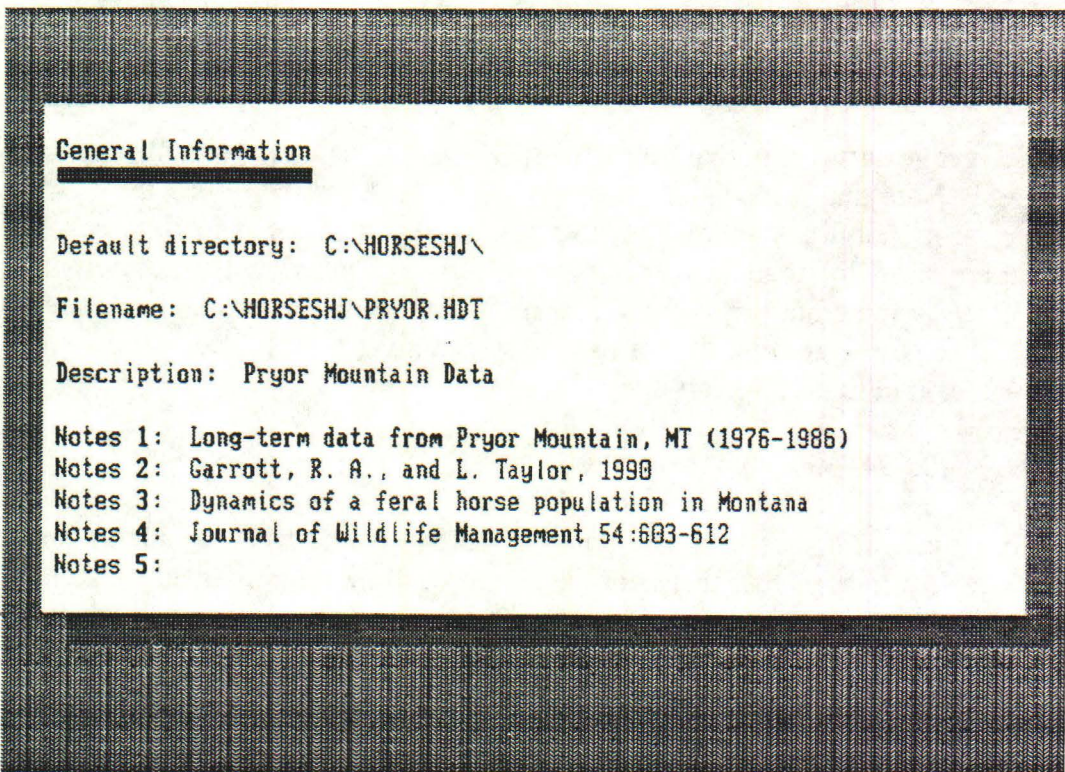
F1 Help | Esc Exit | Use arrows or press highlighted letter to select

Type E to select *Edit Data Set*:



F1 Help | Esc Exit | Use arrows or press highlighted letter to select

Now type G to see *General Information* about this data set.



F1 Help | Esc Done | Enter highlighted letter to modify

This screen shows that the Pryor Mountain data come from a long-term study of wild horses at Pryor Mountain, Montana, reported by Garrott and Taylor in 1990. These are the best demographic data available for wild horses in the western U.S. It's unfortunate that

intensive monitoring of wild horses at Pryor Mountain ended in 1986; the 11 years of data collected prior to that time could have been the basis for a unique long-term record of year-to-year variability in survival and reproduction for a large mammal.

Hit Esc to go back to the previous menu, then type P to see *Survival Probabilities* for Pryor Mountain:

age	males	females	age	males	females
0	0.921	0.948	13	0.957	0.986
1	0.965	0.994	14	0.952	0.981
2	0.965	0.994	15	0.946	0.975
3	0.965	0.994	16	0.936	0.965
4	0.965	0.994	17	0.922	0.949
5	0.965	0.994	18	0.900	0.927
6	0.964	0.993	19	0.866	0.894
7	0.964	0.993	20	0.821	0.845
8	0.964	0.993	21	0.754	0.777
9	0.963	0.992	22	0.663	0.683
10	0.962	0.991	23	0.543	0.560
11	0.961	0.990	24	0.402	0.414
12	0.959	0.988	25	0.000	0.000

F1 Help | Esc Done | Use arrows to move, or enter a new value

This table shows **average** survival probabilities for males and females from each age to the next older age class. Note that these values are very high -- greater than 90% through age 18. Average survival probabilities are also greater for females than for males of each age class and are a little bit less for foals than for 1-year-olds but decrease with age thereafter. The chance of a horse living from birth to a given age can be computed by multiplying the successive probabilities from age 0 up to that age. For example, the chance that a female at Pryor Mountain would live to be 25 years old is

$$(0.948)(0.994)(0.994) \dots (0.414) = 0.064.$$

This program doesn't permit horses to live beyond 25 years old; the fact that such a small proportion reach age 25 indicates that this is not as serious a limitation as it might appear to be.

We won't change any of these data at this time, but try using the arrow keys to move around the screen and hitting F1 to read the help screen for *Survival Probabilities*. When you are ready, hit Esc to go back to the *Edit Data Set* menu. Now type F to see the *Foaling Rates* for Pryor Mountain.

Foaling Rates			
age		age	
0	▶0.000	13	0.470
1	0.000	14	0.470
2	0.000	15	0.470
3	0.410	16	0.470
4	0.410	17	0.470
5	0.410	18	0.470
6	0.550	19	0.470
7	0.550	20	0.470
8	0.550	21	0.470
9	0.550	22	0.470
10	0.550	23	0.470
11	0.470	24	0.470
12	0.470	25	0.470

F1 Help | Esc Done | Use arrows to move, or enter a new value

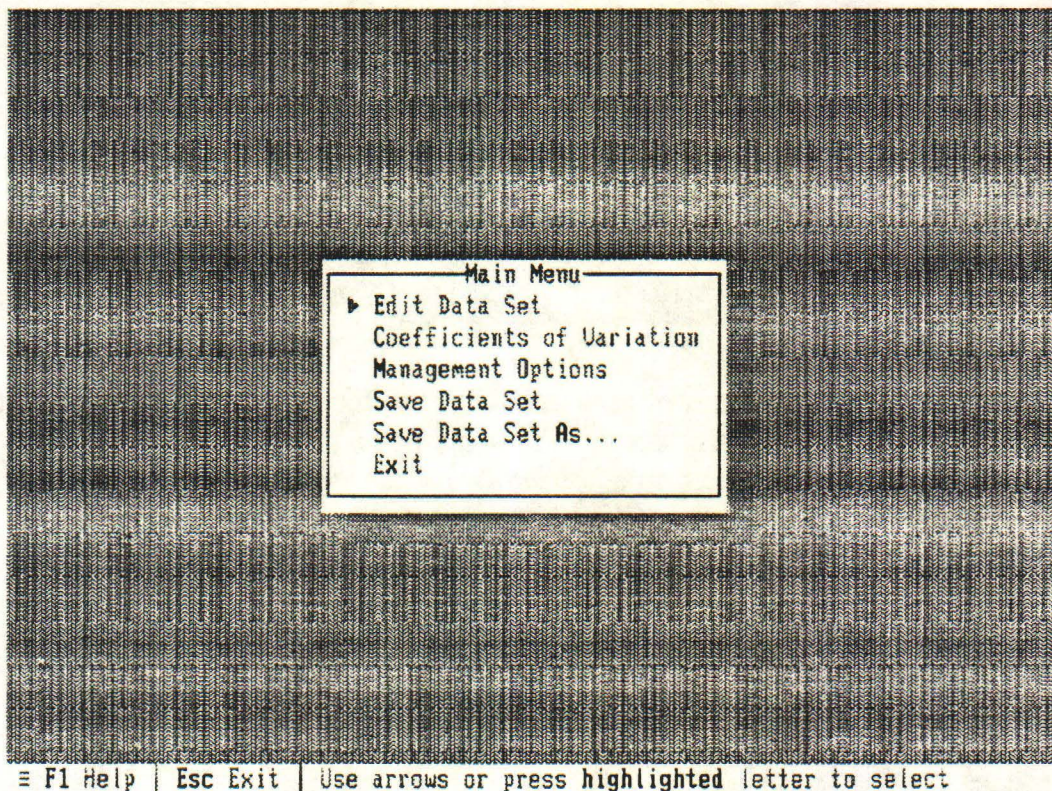
These are average proportions of females of each age that have foals. Note that females at Pryor Mountain produce their first foal at age 3. For some populations, first reproduction occurs at age 2, which would be reflected in a nonzero value adjacent to age 2 in the table. Don't change any data, but hit Esc to go back to the previous menu. Now hit S to see the *Sex Ratio at Birth*:

Sex Ratio at Birth	
Males	▶0.400
Females	0.600

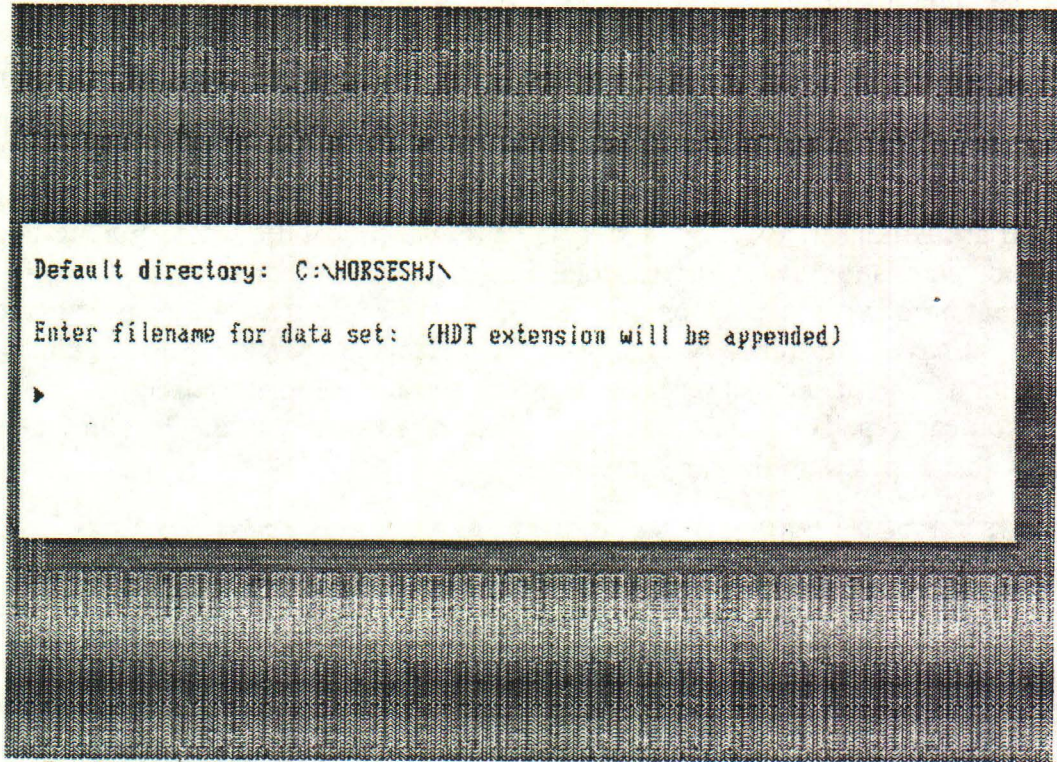
F1 Help | Esc Done | Use arrows to move, or enter a new value

The pointer should be adjacent to the number 0.400, indicating that 40% of foals born at Pryor Mountain were males. Note that the proportion of females among foals born was 0.600. Let's change the sex ratio to 50% males by typing 0.500 and hitting **Enter**. When the proportion of males is changed from 0.400 to 0.500, the proportion of females automatically changes from 0.600 to 0.500, because the total must equal 1.0 (in horses, unlike some organisms, there are only two sexes).

Now hit **Esc** to return to the *Edit Data Set* menu. If you look carefully, you will see a subtle change in the information bar at the bottom of the screen. A new symbol appears in the bottom left corner. This symbol, \equiv , means that the data set has been changed. Let's back up one more level to the Main Menu.



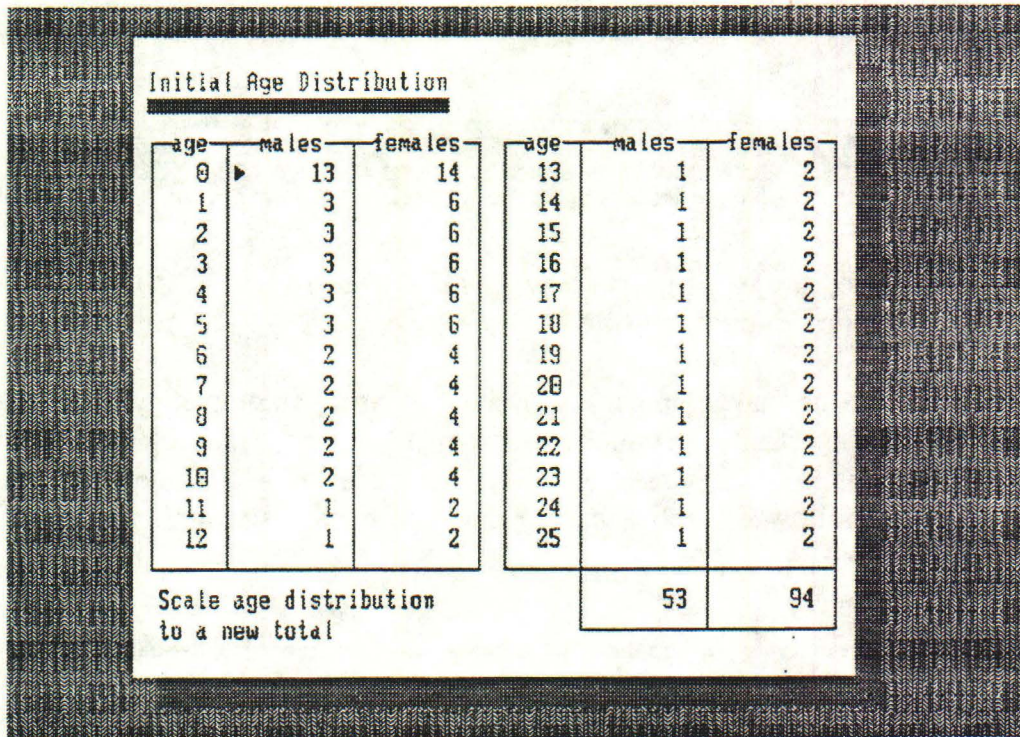
If at this point you typed **S**, for *Save Data Set*, you would overwrite the original Pryor Mountain data set with one that had the same survival probabilities and foaling rates, but a different sex ratio at birth. Unless you want to subvert someone else in your office who is using the same version of the program, you don't really want to do this. If you try it, the program gives you one chance to change your mind before overwriting PRYOR.HDT. Instead, type **A**, for *Save Data Set As*. You'll see the following screen:



≡ Esc Abort | Enter text using Backspace to edit and Enter to accept

Type any legitimate DOS file name (i.e., fewer than 8 characters); for example, PRYORMOD, and your altered data will be saved under that name with HDT added as an extension (e.g., PRYORMOD.HDT) to indicate that the data set is saved in a format unique to the Wild Horse Population Model.

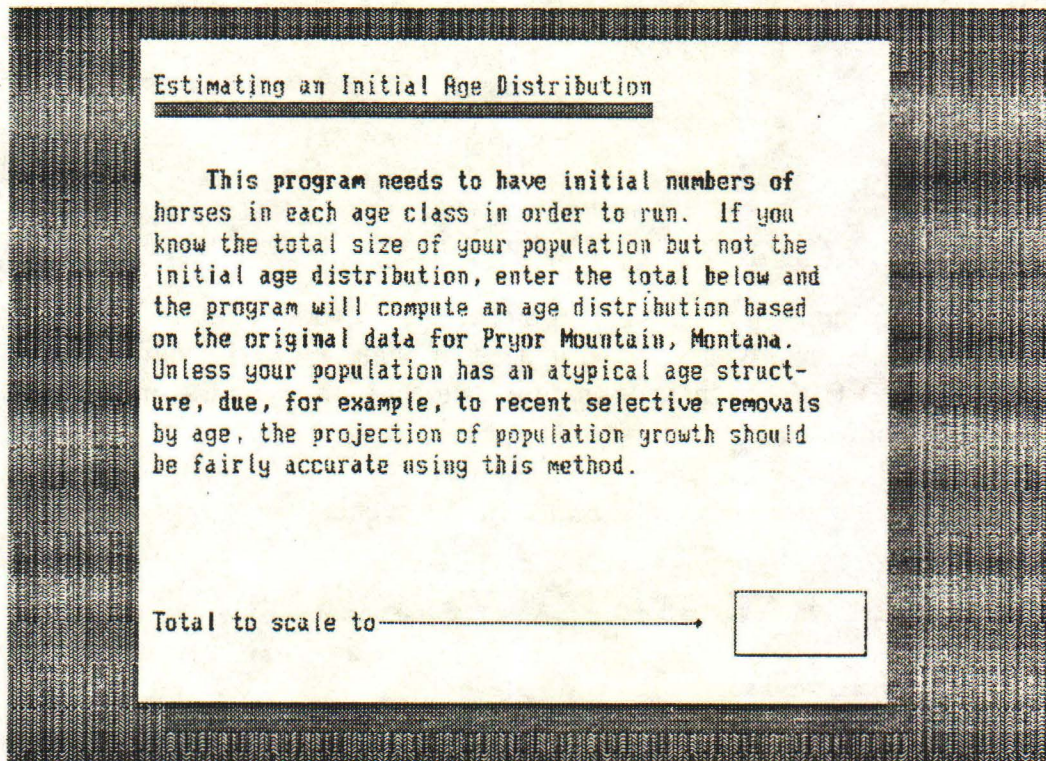
We need to look at one more item in the *Edit Data Set* menu: I, for *Initial Age Distribution*:



≡ F1 Help | Esc Done | Use arrows to move, or enter a new value

This table shows the numbers of males and females in each age class at the start of a simulation. For Pryor Mountain, there were 53 males and 94 females in 1976, distributed approximately as shown among the various age classes (the actual initial age distribution was not reported in the Garrott and Taylor [1990] paper, so I estimated the initial age distribution based on the information they provided).

Suppose you are willing to assume that average survival probabilities and foaling rates are the same for your population as for Pryor Mountain. Suppose further that you don't know the age distribution of your population this year, because horses haven't been gathered and aged, but that you have an estimate of total population size and are willing to assume that the age distribution of your population is the same as a stable age distribution for Pryor Mountain.¹ Then you can type **S** to *Scale the age distribution to a new total*. Try this, and type **100** in the box that appears on the next screen:



≡ Enter a number (0 * 999,999), Backspace to edit, or Enter to accept

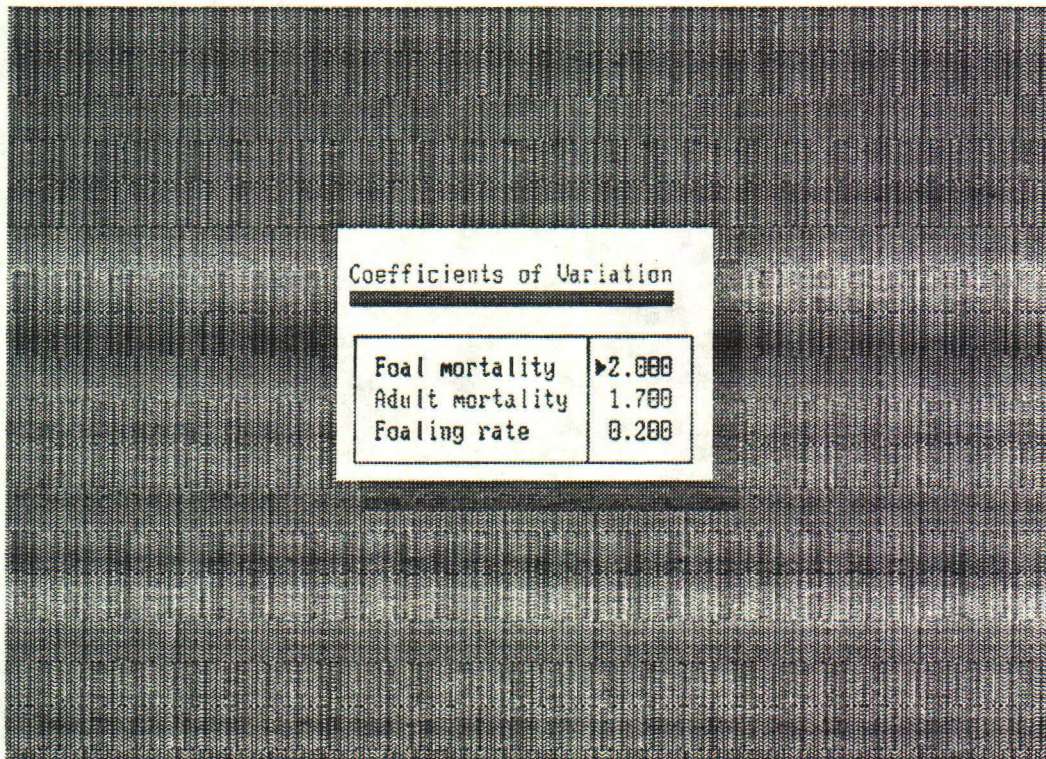
Hit **Enter** to accept this value, and examine the new *Initial Age Distribution*. When you are satisfied, hit **Esc** twice to return to the Main Menu.

Before continuing, let me make one comment about entering a completely new data set. One of the choices on the introductory menu (don't go there now, but look back at the first graphic in this tutorial) is **C** for *Create a New Data Set*. This choice would lead you down the same path we just followed, except that the data entry screens would be filled with

¹A **stable age distribution** is an age distribution that remains the same from year-to-year; i.e., proportions of animals in each age class stay the same, even though total numbers may be increasing at a steady rate. For long-lived animals like wild horses, a stable age distribution may be realized after 20 to 40 years of growth in a constant environment with no management and no density-dependence in mortality or reproduction.

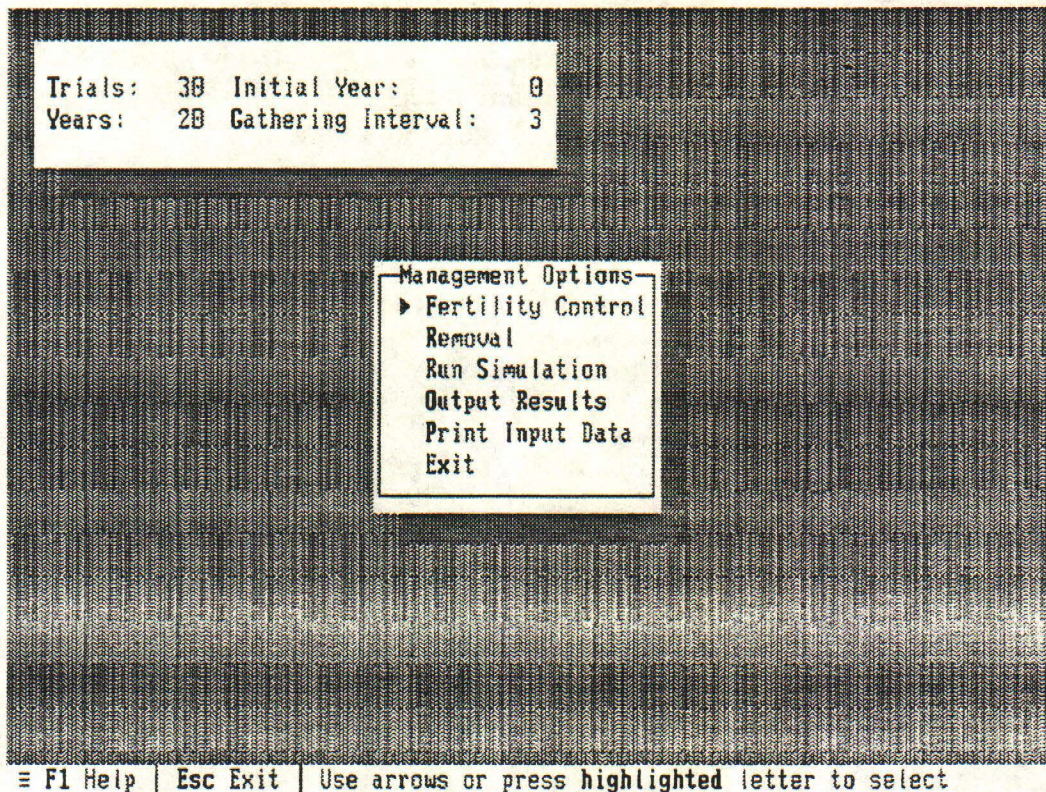
0's instead of the data from Pryor Mountain. You would have to enter your own values for general information, survival probabilities, foaling rates, sex ratio at birth, and initial age distribution or total population size, then save the data set. If you wanted to experiment with a common set of survival probabilities but several different sets of foaling rates, you would enter all the data and save a file, then edit the foaling rates and save a new file with a different name, etc.

Before this digression, we were looking at the Main Menu. Type C, to select *Coefficients of Variation*:



≡ F1 Help | Esc Done | Use arrows to move, or enter a new value

These numbers are indices of year-to-year variation in foal mortality, adult mortality, and foaling rate for the Pryor Mountain population. Read the rather lengthy help file associated with this screen to see what these indices mean, how they are estimated, and how they are used by the program to mimic environmental stochasticity. When you've viewed all four pages of this help file, return to the Main Menu and select M for *Management Options*. You should see the following screen:



We're finally getting to the heart of the program! The box in the upper left corner allows you to set various aspects of the timing of a population simulation. Type any of the highlighted letters and then enter a number to change these values. **T** for *Trials* allows you to specify the number of times a simulation will be run. Because this is a stochastic model, each trial will give different results, as survival probabilities and foaling rates are adjusted upward or downward from their average values in successive years to simulate unpredictable variation in environmental conditions from year-to-year. The maximum number of trials is 50. For this tutorial, change the number of trials to 20 so the program will run a bit faster.

If you type **Y**, you can change the number of *Years* simulated in each trial. The maximum number of years is 50.

I and **G** allow you to set the *Initial Year* of a gather and the *Gathering Interval*, or number of years between successive gathers. At each gather, some horses will be removed and some females treated for fertility control. If the start of your simulation is in 1993, the initial year is 0, and the gathering interval is 3 years, then the first gather takes place in fall 1993 (year 0), the next in fall 1996 (year 3), etc. Try setting the gathering interval to 4 years, but leave the initial year at 0.

Now let's look at the *Fertility Control* menu:

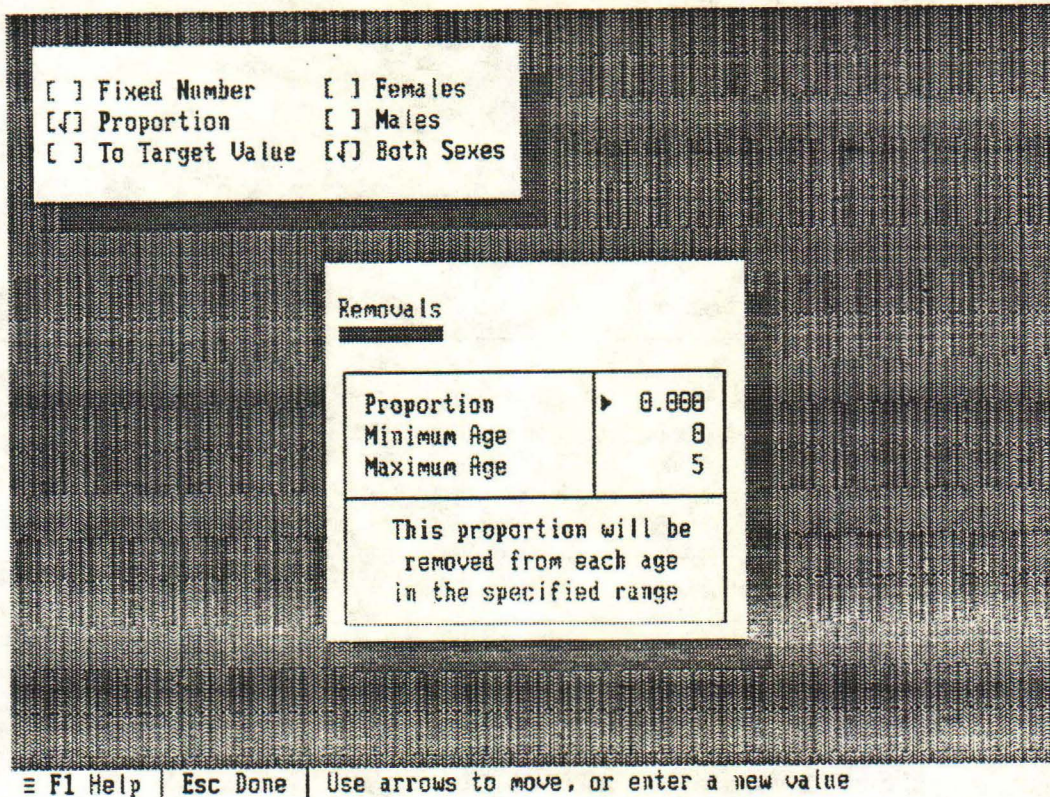
Youngest age for treatment	▶ 0
Oldest age for treatment	25
Proportion not pregnant for 1 year	0.000
Proportion not pregnant for 2 years	0.000
Proportion not pregnant for 3 years	0.000
Proportion not pregnant for 4 years	0.000
Proportion not pregnant for 5 years	0.000
Proportion sterilized	0.000
Total proportion of females treated: 0.000	

≡ F1 Help | Esc Done | Use arrows to move, or enter a new value

In the upper portion of the table, you can set the range of ages of females to be treated at each gather. The default range is from 0 to 25 years; i.e., all females captured will be treated. Leave these values at their defaults for this simulation, and use the arrow keys to move the pointer down into the middle section of the table.

Let's imagine a scenario in which we are able to capture 80% of the females in a population. All of these are treated with an immunocontraceptive that is effective for one year, but 10% of the treated females are permanently sterilized due to an adverse reaction to the drug. This means that the proportion of females not pregnant for 1 year = $0.90 \times 0.80 = 0.72$ and the proportion sterilized = $0.10 \times 0.80 = 0.08$. Enter these values in the appropriate rows of the table. Note that the total proportion of females treated is shown as 0.80, as we specified initially.

Now that specifications for fertility control have been set, hit **Esc** to return to the previous menu, then type **R** to set *Removal* options.



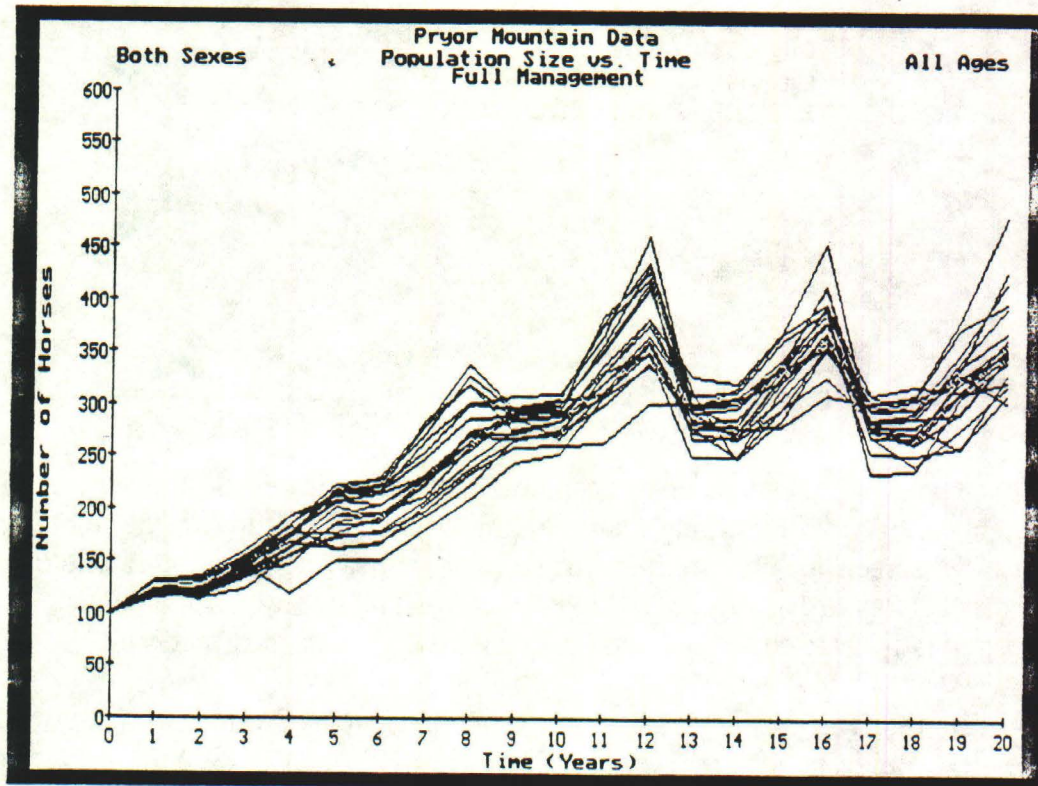
The box in the upper left portion of the screen gives you a choice of removing males only, females only, or both sexes at each gather. It also allows you to choose among three ways of determining how many horses are removed. *Fixed Number* means that a constant number of horses will be removed at each gather, provided there are enough horses present within the age range specified in the box in the center of the screen. If there aren't enough horses in this age range, then all horses within the age range will be removed. *Proportion* means that a constant proportion of horses will be removed from the specified age range at each gather. *To Target Value* means that the population will be reduced to the target value at each gather, although horses older than the indicated top removal age will not be taken even if the target value can't be reached by removing all animals within the specified age range. For this tutorial, type **T** to select the option of removing horses to a target value.

Note that the headings in the box in the center of the screen have changed, reflecting the fact that you want to remove horses to a target value rather than removing a fixed number or proportion of the population. Enter **250** as the target value.

The minimum and maximum ages of horses to be removed are set at 0 and 5 for this run, but could be changed to any values you wish. You may also choose to expand the age range of removals upward if necessary. This means that if the target for population left on the range is not met by just taking horses between the minimum and maximum age, additional horses will be taken from an expanded age range. For this run, type **E**, and then enter **9** as the top removal age.

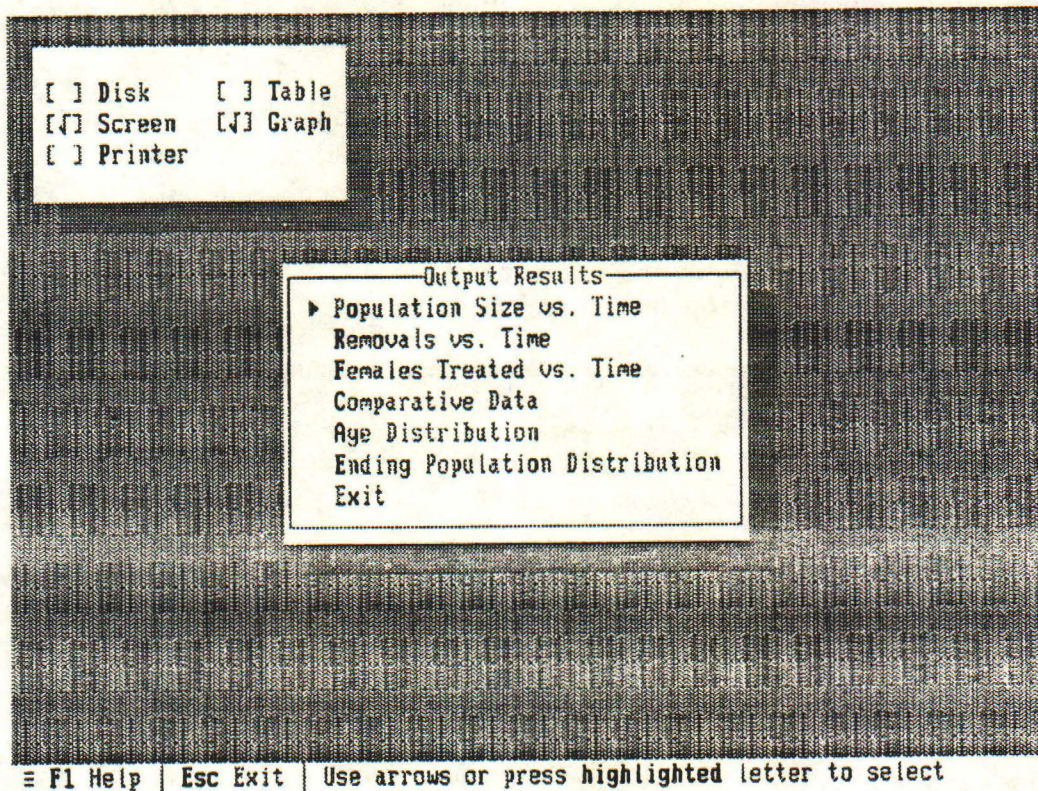
Now that options for fertility control and removals have been set, hit **Esc** to return to the *Management Options* menu. The next step is to type **S** to *Run a Simulation*. After a brief delay for initial calculations to be made, a graph like the one below of population size

vs. time will appear on the screen. The actual results of your run will be different from those shown here because this is a stochastic model with mortality and foaling rates selected at random each year. Each blue line in this "spaghetti graph" represents a different trial; the output illustrates the range of possible outcomes of population growth taking potential year-to-year variation in environmental conditions into account. Note the label "Full Management" in the heading of this graph. This means that the graph shows population growth with both periodic removals and fertility control implemented according to the schedule you specified. The program is also calculating how the population will grow with no management, with removals only, and with fertility control only. You will be able to see the results of these calculations in a few moments. For the time being, make a mental note of the range of ending population sizes for the full management case.



When you have finished viewing this output, hit any key to return to the *Management Options* menu. Before seeing the results summarized in various ways, it may be useful to print a copy of the input data, i.e., survival probabilities, foaling rates, management options, etc. used for this simulation. To do so, type **P** for *Print Input Data*, then (if your printer is connected and turned on), **P** again at the next screen (this menu is not shown because you should be getting used to the process by now).

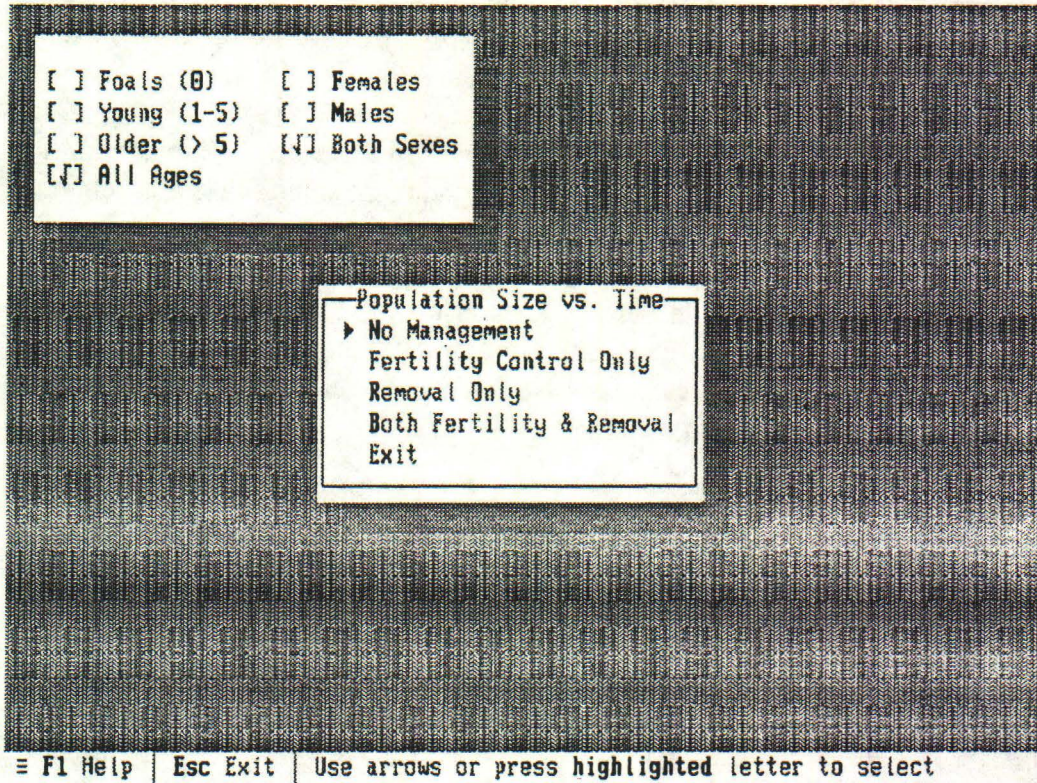
At the *Management Options* menu, type *O* to *Output Results*, and you will see the following screen:



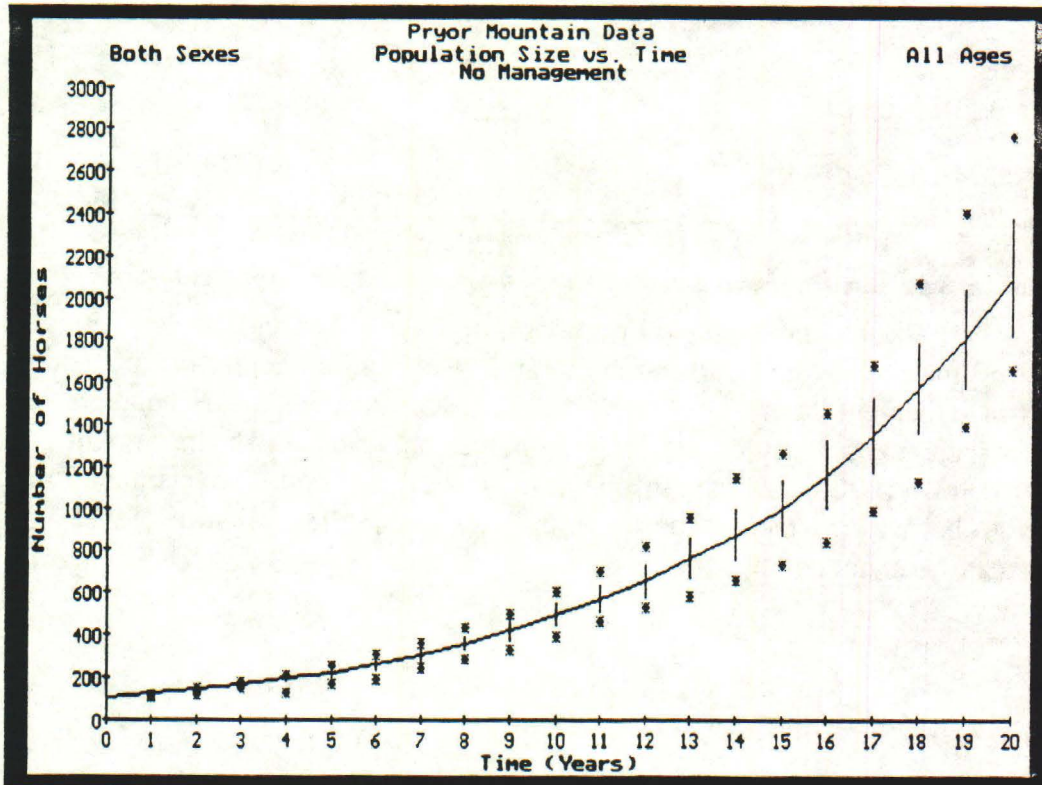
All results can be displayed in either tabular or graphical form and viewed on the screen, saved to a file, or sent to a printer by typing the highlighted letter in the box in the upper left corner. We will use the screen for all output in this tutorial, but saving output in a file or printing it is fairly straightforward -- just follow the directions that appear on the screen when one of these options is selected, or use the on-line help for more information.

The main menu lists the six types of output that can be displayed. *Population Size vs. Time* shows changes in average population size over time for each of the following cases: no management, fertility control only, removal only, and full management (fertility control plus removal). *Removals vs. Time* and *Females Treated vs. Time* summarize data on number of horses removed and number of females treated, respectively. *Comparative Data* shows population sizes at a specified time side-by-side for the four management cases (no management, etc.) so different management options can be compared. *Age Distribution* shows the average proportion of horses in each age class at the end of the simulation. *Ending Population Distribution* shows cumulative frequency distributions of final population sizes for the four management cases.

Type o to see a graph of *Population Size vs. Time*. This brings up yet another menu screen:



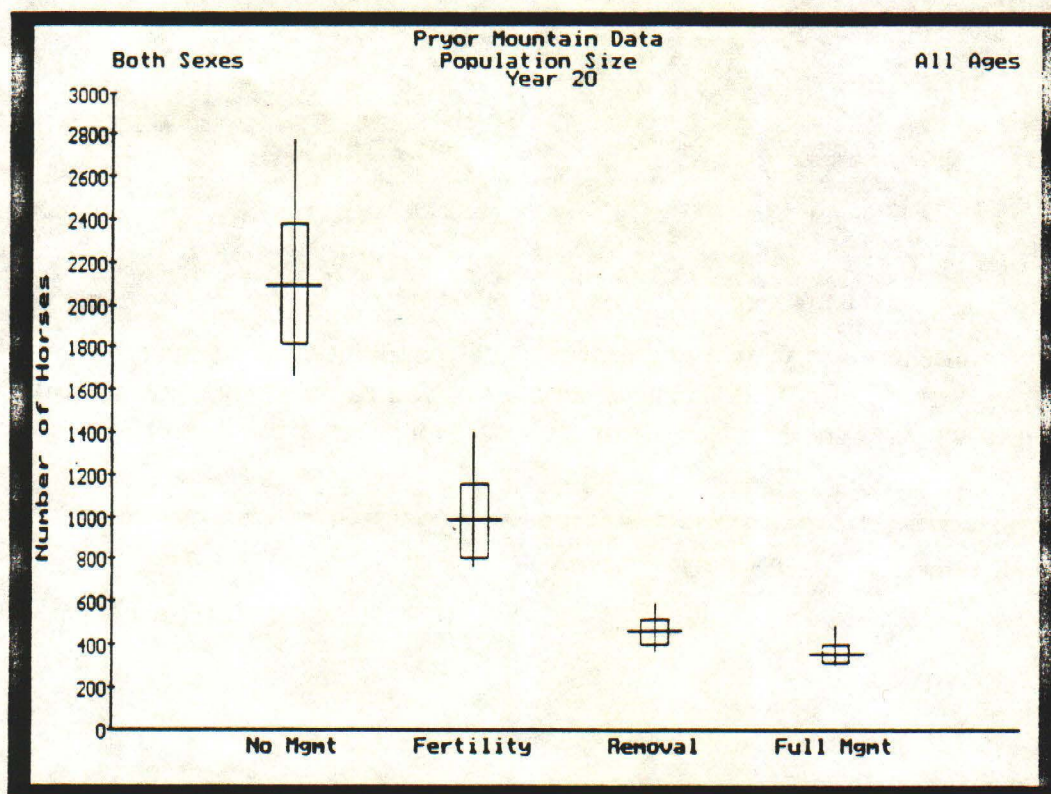
As you can see, you can choose to view a graph of the total population (all ages and both sexes, the default), or a graph of a particular age/sex class. You can also select a particular management option to view. Type N to see a summary of population growth with *No Management*.



In this graph, the broken blue line shows average population size for each year of the simulation, the vertical blue lines represent means \pm 1 standard deviation for each year, and the red asterisks represent minimum and maximum population sizes for the set of trials that were run. How does the range of ending population sizes for this case compare with the range for full management from the spaghetti graph?

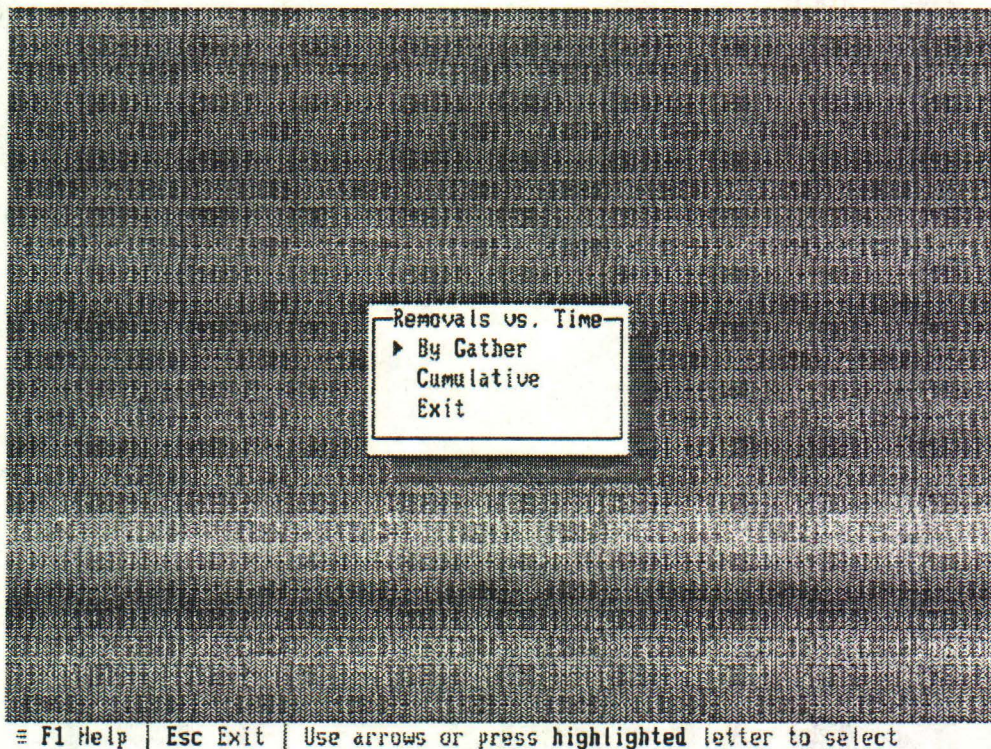
When you are finished looking at this graph, hit any key to return to the *Population Size vs. Time* menu. If you wish, view graphs for the other management cases, or change the age or sex to see a subset of the total population. When you are done experimenting, be sure the age class is set to **A** for *All Ages* and the sex to **B** for *Both Sexes* before continuing. Then hit **Esc** (or **x** for *Exit*) to return to the Output Results menu.

The next thing we'll look at is *Comparative Data* -- type **C** to do this, then from the next menu (not shown here), **P** for *Population Size*.

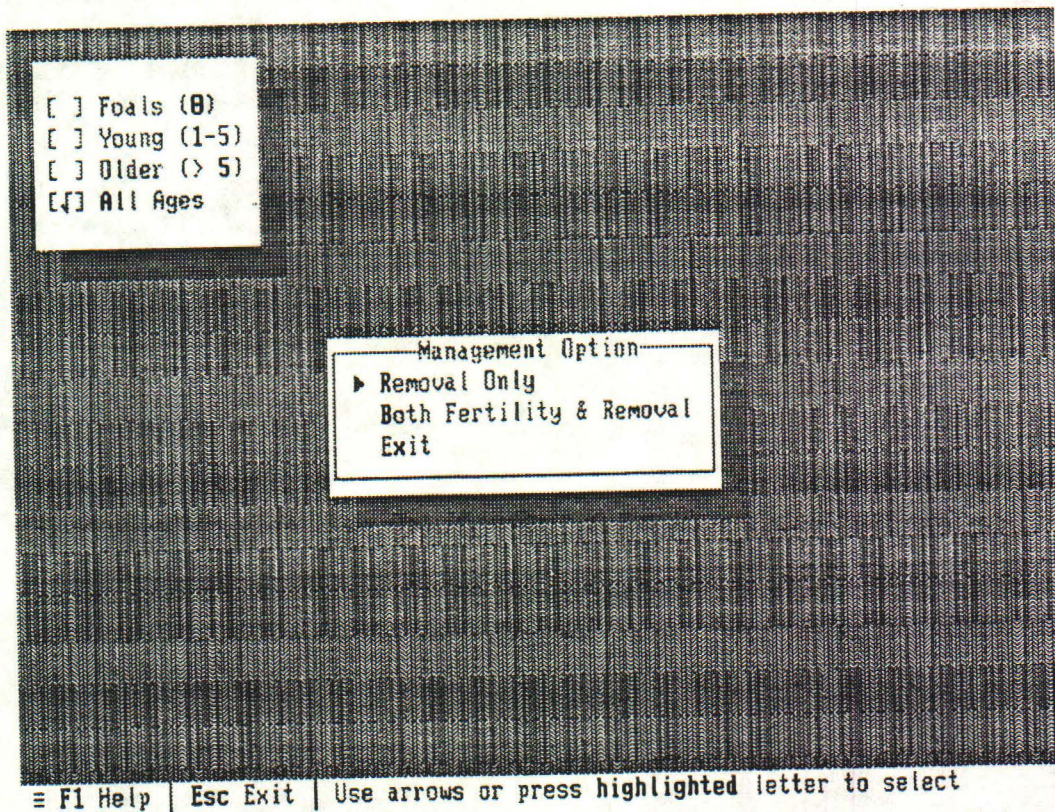


This graph shows average population sizes (horizontal blue lines), \pm standard deviations (tops and bottoms of blue rectangles), and minimum and maximum population sizes (ends of red lines) for each management case. This graph makes it easy to compare population growth with no management, fertility control only, removal only, and full management. Results are displayed for a particular year, in this case year 20, the end of our simulation. If you hit any key to go back to the menu, you'll see that the year to be shown in the comparative graph can be changed.

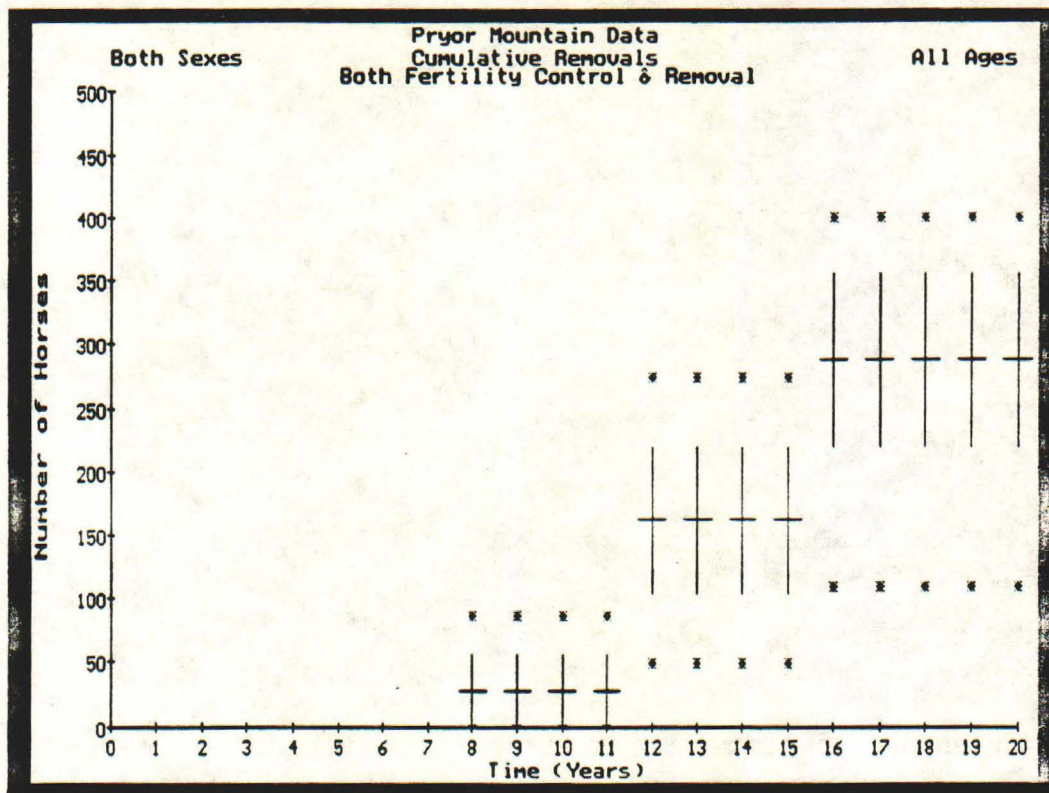
Return to the *Output Results* menu and let's examine *Removals vs. Time* (type R). You will see the following screen:



By Gather will show numbers of horses removed at each gather, *Cumulative* will show cumulative numbers removed over time. For example, if 50 horses are removed in year 0, none in years 1 and 2, and 100 in year 3, then cumulative numbers removed are 50 in year 0, $50+0 = 50$ in year 1, $50+0+0 = 50$ in year 2, $50+0+0+100 = 150$ in year 3, etc. Type C to see cumulative removals.



The next choice is to look at removals for the *Removal Only* option or the full management option. We can also select an age class to display. Let's view the output for *Both Fertility (Control) and Removal (B)* option, for *All Ages (A)*.



The blue lines and red asterisks mean the same thing here as in the population size vs. time graphs. Because we aren't removing animals until the population exceeds a target value, there may be few or no removals shown until year 8 or later. Because gathers to remove horses were made at four year intervals, the cumulative number removed remains the same from year 8 through 11, then increases to a new level at year 12 and remains the same until year 16, etc.

Hit any key to exit this graph, then Esc twice to go back to the *Output Results* menu. Output for *Females Treated vs. Time* is similar to that for removals, so won't be covered in this tutorial. Having seen a few graphs, we should look at some tabular output. Type T to select *Table*, then C for *Comparative Data*. From the next menu (not shown here), type P for *Population Size*.

Both Sexes		Pryor Mountain Data Management Comparisons Year 20			All Ages
	No Mgmt	Fertility Control	Removal	Full Mgmt	
POPULATION SIZE (Both sexes)					
Mean	2094	980	459	361	
SD	286	173	55	43	
Min	1667	763	362	304	
Max	2768	1395	586	479	
CUMULATIVE FEMALES TREATED					
Mean	0	724	0	474	
SD	0	89	0	23	
Min	0	583	0	442	
Max	0	885	0	524	
CUMULATIVE REMOVALS (Both sexes)					
Mean	0	0	532	287	
SD	0	0	73	69	
Min	0	0	391	110	
Max	0	0	693	401	

≡ F1 Help | Esc Done |

This table shows not only population size but also cumulative number of females treated and cumulative number of animals removed in year 20. As noted earlier, the numbers you see on the screen will not be the same as those shown here because each run uses a different sequence of random numbers and so gives different results. You could use this table to compare the cost and effectiveness of fertility control only, removal only, and fertility control plus removal as management strategies. How much do each of these strategies reduce average population size below that for no management? How much variation is there in projected population size in year 20 for each of these strategies? How many animals are treated and removed in each case? If you have data on costs of fertility treatment and removal, you could compare total projected cost of each management strategy.

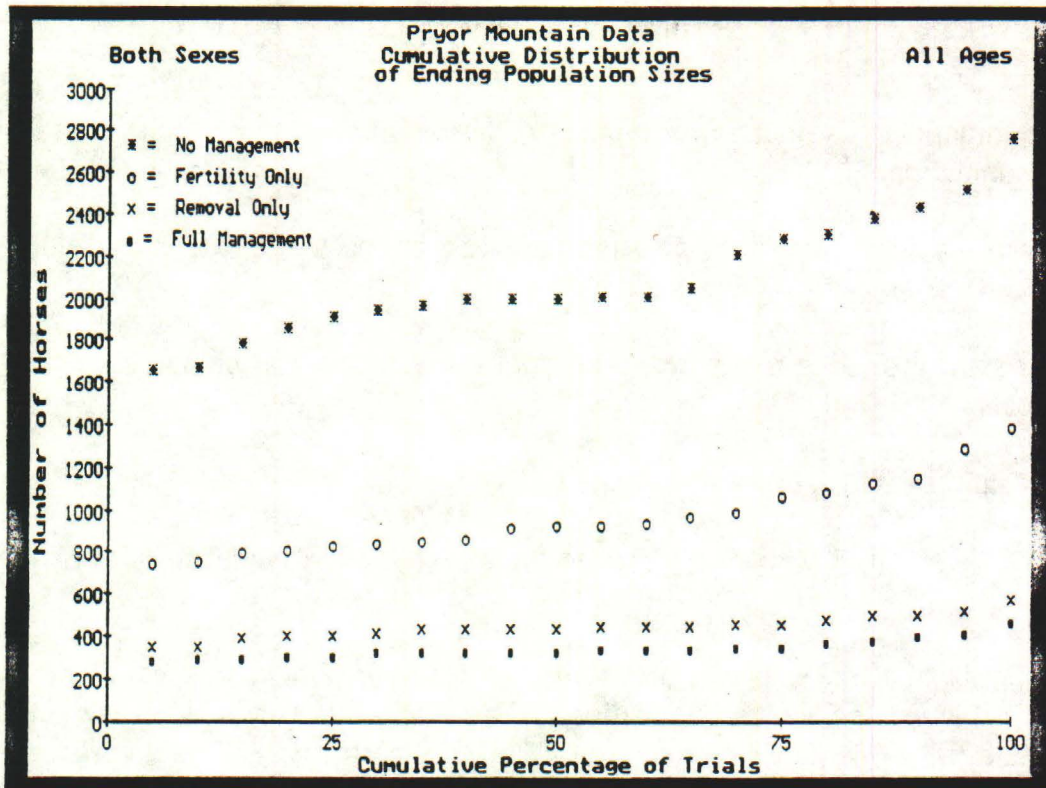
Hit Esc twice to return to the *Output Results* menu. With output format still set at T for *Table*, type A to see the average *Age Distribution* of the population at the end of the simulation.

Pryor Mountain Data				
Both Sexes	Age Distribution			All Ages
Year 20				
Age Class	No Mgmt	Fertility Control	Removal	Full Mgmt
0	16.0%	15.5%	16.5%	15.8%
1	13.5%	13.9%	13.7%	13.5%
2	10.6%	1.7%	12.1%	1.8%
3	9.7%	10.0%	12.5%	11.6%
4	7.9%	9.1%	3.3%	5.3%
5	6.7%	8.4%	2.9%	5.0%
6	5.8%	1.3%	2.8%	0.8%
7	4.9%	6.0%	2.4%	3.9%
8	4.0%	5.6%	0.8%	2.2%
9	3.6%	5.3%	0.7%	1.9%
10	3.1%	1.0%	2.9%	1.0%
11	2.5%	3.8%	2.5%	3.9%
12	2.2%	3.7%	1.3%	3.1%
13	1.9%	3.2%	1.3%	3.0%

≡ F1 Help | Esc Done | Use arrows to scroll

This table shows the percentage of animals of each age in year 20 for each management case. Use the arrows to scroll up and down to view all 26 age classes. Note the smaller percentage of 2-year-olds in the fertility control and full management cases than in the other two cases. The reason for this is that we scheduled fertility control at four-year intervals starting in year 0. This means that the last fertility control before the end of the simulation (year 20 in this case) occurred in year 16. Females treated in the fall of year 16 would already have been pregnant, and so would have produced foals at the normal rate in year 17. Because our contraceptive treatment was effective for one year, many fewer females than usual would have gotten pregnant in year 17, so foal production would be depressed in year 18. Foals born in year 18 would be 2-years-old in year 20, accounting for the low frequency of this age class in the population. Voilà!

Return to the *Output Results* menu to view one last form of output. Type G to set the output format back to graphical, then E for *Ending Population Distribution*.



Based on comments of BLM personnel who tested version 1.0 of this program, this is one of the more confusing forms of output. Its purpose is really to show the range of variability in population size at the end of a simulation, due to the stochastic nature of the model. Note that the horizontal axis is not time, but cumulative percentage of trials. As explained previously, each trial yields a different result because different sequences of random numbers are drawn to simulate year-to-year variability in environmental conditions. Consider the no management case for example. The leftmost red asterisk on the graph is the minimum ending population size with no management for the 20 trials we ran. The rightmost red asterisk is the maximum population size with no management for these 20 trials; i.e., 100% of trials had ending population sizes less than or equal to this value. The remaining red asterisks show all the rest of the trials, with intermediate ending population sizes. Find the red asterisk above the 50% position on the x-axis. The corresponding point on the y-axis is the median population size; i.e., 50% of ending population sizes were below this value and 50% were above it. You could do a similar analysis for each of the cases in which management was applied. What this graph can show that can't be discerned from the other tables or graphs is that there may be only a few trials with extremely high or extremely low ending population sizes.

This is the end of the tutorial. Hit Esc or x for *Exit* several times in succession to quit the program. I hope you enjoy using the program.

DATA REQUIREMENTS

This program requires five sets of data about a population in order to do a simulation:

- (1) the initial age distribution, or number of horses in each age/sex class at the start of a simulation.
- (2) survival probabilities for males and females from each age to the next older age.
- (3) age-specific foaling rates; i.e., proportions of females of each age class that produce foals.
- (4) sex-ratio of foals at birth.
- (5) coefficients of year-to-year variation for foal mortality, adult mortality, and foaling rate.

You may not have all these pieces of information for your population, in which case you will have to use values for another population and assume yours is similar or try to make reasonable guesses to fill in the holes in your data. This is a perfectly reasonable procedure as long as you don't assume that the output of the model is exactly what will happen in your population. A good strategy for using the program would be to explore the sensitivity of the results to variation in parameters for which you don't have solid data, and focus future efforts at data collection on those parameters that have the greatest effect on population growth.

Initial Age Distribution

It should be fairly straightforward to get an accurate initial age distribution for your population, if most of the population is gathered and individuals are sexed and aged at the beginning of a study. Although precise aging of animals greater than 10 years old is problematic (Garrott 1991), this shouldn't unduly influence population projections unless age estimates are systematically biased upward or downward.

You may only have data on total population size at the beginning of a study, if no gathers have been done recently. The program includes the option of calculating an age/sex distribution based on a total population size entered by the user. If you select this option, the stable age distribution for Pryor Mountain is used together with the total population size you enter to compute an initial age distribution for simulating population growth for your population. In the Pryor Mountain stable age distribution, for example, there would be 11% female foals, so if your total population were 200, 22 animals would be classified as female foals. See the information screen that appears when you select this option in the program, as well as the tutorial above, for more discussion of the validity of this approach.

Survival Probabilities

Of the fundamental demographic parameters of a population, survival probabilities are often the most difficult to get, especially for long-lived animals such as wild horses. There is a tradition in wildlife biology of converting age ratios collected at one point in time (e.g., from hunter check stations for deer or roundups of horses) into survival probabilities (Caughley 1974, 1977, Eberhardt 1988, Jenkins 1989). However, if a population is increasing or decreasing in size, this procedure systematically underestimates or overestimates survival probabilities, respectively. Only if a population is constant in size and has remained so for a fairly long time (30-40 years for horses), will the ratios of animals in successive age classes equal survival probabilities. Since the purpose of estimating survival probabilities is usually to build a model to predict potential growth rate of a population, assuming growth rate = 0 in order to calculate survival probabilities is a serious problem!

Here is an example to illustrate why survival probabilities can't be estimated from a standing age distribution without also knowing the population growth rate. Suppose there are 100 one-year-olds and 80 two-year-olds at a census of the population in 1993. If the population is not growing and has been constant long enough to achieve a stable age distribution, then there would have been 100 one-year-olds in 1992, and so the survival probability from age 1 to age 2 = $80/100 = 0.80$. But if the population is growing at 12% per year, then there would have been only 89 one-year-olds in 1992 ($1.12 \times 89 = 100$), and the survival probability from age 1 to age 2 would be $80/89 = 0.90$. Conversely, if the population is decreasing at 12% per year, there would have been 114 one-year-olds in 1992 ($0.88 \times 114 = 100$), and survival probability of one-year-olds would be $80/114 = 0.70$. This shows that a ratio of number of two-year-olds to number of one-year-olds of 0.80 at a given point in time is consistent with survival probabilities for one-year-olds ranging from 0.70 to 0.90 (if we assumed higher or lower growth rates, the range of survival probabilities would be even greater). Thus, although age distribution data are relatively easy to obtain (for example, Garrott [1991] presents age distributions for three sets of horses totalling more than 60,000 animals), these data cannot be translated into survival probabilities as wildlife biologists are often tempted to do.

To get accurate estimates of survival probabilities for wild horses requires keeping track of known individuals over time, to see how long they live. This could be done by gathering a population, aging and marking all individuals, and then following the fates of those individuals over several years, either by intensive field observations or subsequent gathers. If this population model stimulates just one BLM district to set up such a long-term monitoring program, I will consider it a success.

Foaling Rates

Foaling rates are in principal much easier to estimate than survival rates, because they don't necessarily require long-term monitoring of a population. You should bear in mind, however, that foaling rates used by the program are proportions of females of each age class that actually give birth. Therefore pregnancy rates assessed by visual observation, palpation, or hormonal assays (Wolfe et al. 1989, Garrott et al. 1991, Kirkpatrick and Turner 1989) may underestimate foaling rates if done too early in the "reproductive year", before all females have mated, or may overestimate foaling rates if done in the middle of the gestation period because they don't account for fetal losses prior to birth.

Sex Ratio

The program also needs to know sex ratio at birth. This can be estimated by determining sexes of a sample of foals in a population at or shortly after birth. Lacking this information, a sex ratio of 50% male: 50% female could be assumed (although the sex ratio among foals at Pryor Mountain was 40% male: 60% female).

Coefficients of Variation

You may be discouraged by all the data needed to use a population model such as this, but there is one more feature of the model for which it is even more difficult to obtain appropriate data. In discussing survival probabilities and foaling rates above, I have considered variation with age, but not variation from year to year. Yet a realistic model should account for the fact that bad weather in some years may depress survival and foaling rates below average values whereas favorable conditions in other years may increase these rates. This program incorporates such unpredictable variation in environmental conditions by modeling population growth as a stochastic process. It uses coefficients of variation in foal mortality rate, adult mortality rate, and foaling rate to calculate different survival probabilities and foaling rates for each year of a simulation. To estimate these coefficients of variation requires long-term studies such as those at Pryor Mountain, Montana (11 years; Garrott and Taylor 1990), the Granite Range, Nevada (6 years; Berger 1986), and Assateague Island, Maryland and Virginia (8 years; Keiper and Houpt 1984).

If you have long-term demographic data for a population, then the coefficient of variation (CV) for a parameter is the standard deviation divided by the mean value of that parameter. Note that the program uses mortality rates instead of survival probabilities in these computations (mortality rate = 1 - survival probability). For example, if adult survival probabilities (all age classes combined) in five years are 0.95, 0.90, 0.75, 0.95, and 0.85, then corresponding mortality rates are 0.05, 0.10, 0.25, 0.05, and 0.15. Mean mortality rate is 0.12 and the standard deviation of mortality rate is 0.08, so the coefficient of variation = $0.08/0.12 = 0.67$.

Lacking long-term demographic data, you may use coefficients of variation for Pryor Mountain, which are the defaults for the program. These CV's are quite large (greater than 1 for both foal and adult mortality rate), reflecting the fact that there was one very bad winter at Pryor Mountain when mortality rate increased from less than 10% to about 50%. Alternatively, you may set CV's at 0, to run a simulation without environmental stochasticity. An interesting experiment is to see how population growth responds to variation in coefficients of variation. With high CV's, the range of ending population sizes will clearly be greater. How do high CV's influence average ending population sizes? Which has the strongest influence: a high coefficient of variation in adult mortality, foal mortality, or foaling rate? In making these comparisons, keep in mind that the maximum possible value of foaling rate CV is less than maxima for foal and adult mortality rates, because the mean is greater for the former and CV's depend on both the mean and standard deviation of a parameter. The maximum for foaling rate is probably about 0.5, whereas maxima for mortality rates are in the range of 2 to 3.

MANAGEMENT OPTIONS

With one exception, the program is quite flexible in the range of management options that can be specified by the user. The program implements management by simulating gathers at regular intervals. At each gather, horses of one or both sexes are removed from the population and females to be released back are treated with a contraceptive, assuming you set conditions for removal and fertility treatment. The program not only keeps track of what happens to the population under full management (both removal and fertility control), but also what would happen if removal only were applied, fertility control only were applied, or there were no management.

Before running a simulation, you specify the schedule of gathers; i.e., the initial gathering year and the interval between gathers. You don't have the option of varying the gathering schedule or conditions for fertility treatment and removal in the middle of a simulation. For example, if gathers were initially scheduled for every three years, you aren't able to postpone the gather scheduled for year 6 if the population is smaller than expected at that time. There are two reasons for this limitation: (1) to do otherwise would have made the program much more complex, and (2) because this is a stochastic model, an unexpectedly low (or high) population size in a particular year may result from random environmental variation rather than an ill-timed gather. The best use of the program is not to let it determine optimal management decisions for you but to use it for experiments to learn how various management choices interact with demographic characteristics of a population and stochastic environmental variation to influence population growth.

Fertility Control

Pilot studies are currently (1993) underway to determine the effectiveness in the field of an immunocontraceptive developed by Turner, Kirkpatrick, and colleagues (Liu et al. 1989, Kirkpatrick et al. 1990, Turner and Kirkpatrick 1991). In captive animals, this contraceptive prevents pregnancy for about one year. This is represented in the program by specifying the proportion of females not pregnant for one year in the fertility control menu. If you thought all females could be captured and treated successfully, this proportion would be 1.0; more realistic would be a value less than 1.0 to account for females not captured at the gather and females for whom the treatment doesn't work.

You will soon discover from running the program that a one-year contraceptive applied at intervals of three or more years doesn't stabilize population size. Therefore you have the option of simulating the effects of longer-lasting contraceptives on population growth. If current research designed to lengthen the lifespan of immunocontraceptives is successful, or if BLM reconsiders the use of hormonal implants which can prevent pregnancy for several years (Eagle et al. 1992, Garrott et al. 1992, Plotka et al. 1992), then simulations with longer-lasting contraceptives will reflect viable management options.

Removal

The program enables you to simulate three basic patterns of removing horses from a population: remove a fixed number at each gather, remove a constant proportion of the animals at each gather, or reduce the population to a target value (carrying capacity) at each

gather. Reducing the population to a target value is probably most similar to actual management practice, because such target values are calculated for each Herd Management Area based on forage availability and other factors. Removing a fixed number or constant proportion might make sense if the major reason for management had to do with the disposition of horses once they were removed instead of maintaining a population at a specified level on the range.

Removing horses to a target value is a form of adaptive management, even though gathers occur at pre-established time intervals. The number of horses to be removed is calculated at each gather based on the population size at that time and the target value. If the population is below the target value, no horses will be removed. If the population is above the target value and the age range for removal is set at 0 to 25, then the number of horses removed = population size - target value. If a more limited age range for removal is specified, then the population won't be decreased to the target value at each gather unless there are enough horses in this age range to do so.

HOW THE PROGRAM WORKS

Any computer program uses three fundamental process to do its job: **sequential** operations, **repetitive** operations, and **branching** based on values of decision variables. I'll describe how this program works in terms of these three processes.

Once data have been entered and management options set, the program computes effective foaling rates for each year before running a simulation. These effective foaling rates are reduced from mean foaling rates for some age classes and some years according to the fertility control parameters entered by the user. This is not a straightforward process. For example, suppose the initial gathering year is year 0, the gathering interval is 3 years, females of all ages are treated at each gather, 70% of females present in a population at a gather are prevented from becoming pregnant for one year, and 10% of females present at a gather are permanently sterilized due to an adverse reaction to treatment. The first year in which foaling rates are reduced is year 2, because females treated in year 0 are already pregnant with a foal to be born in year 1. Eighty percent (70% + 10%) of females treated in year 0 don't become pregnant in year 1 and so don't have foals in year 2. Thus if the mean foaling rate for 3-year-olds in the absence of fertility control is 0.47, the effective foaling rate of this age class in year 2 is $(1 - 0.80) \times 0.47 = 0.094$.

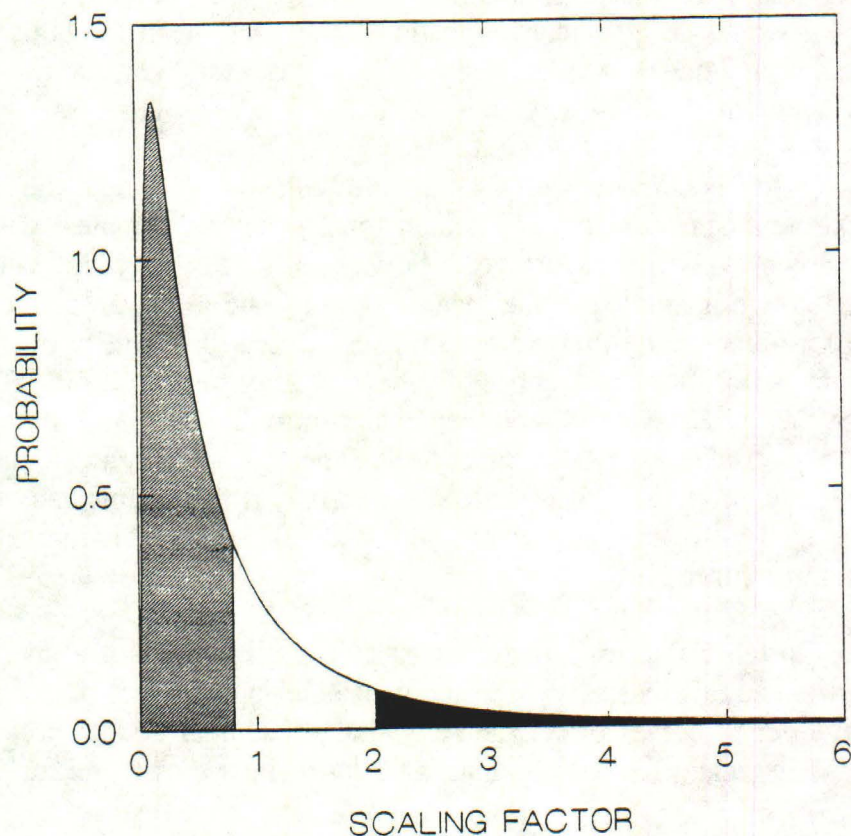
In years 3 and 4, mean foaling rates of mares treated in year 0 are reduced by 10%, because that many animals were sterilized by the initial treatment. But mares which are 3-year-olds in year 4 weren't born yet in year 0, so weren't treated, so their foaling rates are not reduced. By year 5, the treatment at the second gather in year 3 takes effect. But the program has to account for the fact that 10% of mares older than five were sterilized by the initial treatment, so retreatment of these mares in year 3 doesn't further reduce their fecundity. Part of the reason for requiring the user to specify the gathering schedule in advance was the complexity of designing this routine for computing effective foaling rates.

The steps described below are repeated for each year of a trial, and then for each trial of a simulation run. Results are different for each trial because random numbers are used to

simulate environmental and demographic stochasticity (these concepts are described more fully below). The population is censused in summer, immediately after the foaling season, and so for purposes of the model each year goes from mid-summer to mid-summer, say July 1st to the following June 30th. Here are the steps that are performed in sequence for each year:

(1) If this is a gathering year, the number of horses to be removed is calculated and each age/sex class within the age range specified is reduced proportionally so that the total number of horses removed equals the calculated number. If the calculated number to be removed exceeds the total in this age range, then these age/sex classes are reduced to zero but additional horses are not removed to make the calculated number. In other words, limiting removal to the specified age range takes priority over removing the necessary number of animals to meet a target value for population size.

(2) Next, a scaling factor is calculated which will be multiplied by the mean mortality rate of each age class to simulate environmental stochasticity. This scaling factor is selected at random from a lognormal distribution with a mean of 1 and a standard deviation (SD) equal to the coefficient of variation (CV) of adult mortality rate supplied by the user (since $CV = SD/\text{mean}$, $SD = CV$ when the mean = 1). A lognormal distribution is one in which the logarithms of a set of numbers are normally distributed, i.e., exhibit a bell-shaped curve. If the numbers themselves, rather than their logs, are plotted on the x-axis, the distribution will have an extended right tail compared to a normal distribution which is symmetrical around the mean. The reason for using a lognormal distribution to simulate environmental stochasticity is that such a distribution fits the Pryor Mountain data fairly well, and there are no other records of mortality rates for wild horses as long as the 11 years of data for Pryor Mountain. A lognormal distribution with mean = 1.0 and SD = 1.7 (reflecting year-to-year variation in adult mortality rate at Pryor Mountain) looks like this:



The probability of picking a scaling factor less than 0.8 is the hatched area under the curve to the left of 0.8 on the x-axis; this probability = 0.656. The probability of picking a scaling factor greater than 2.0 is the shaded area under the curve to the right of 2.0 on the x-axis: 0.116. The probability of picking a scaling factor between 0.8 and 2.0 is the area under the curve between 0.8 and 2.0 on the x-axis: 0.228. Other probabilities can be determined similarly. An example of a random sequence of 19 scaling factors selected from this distribution is 0.86, 4.81, 6.24, 0.15, 3.72, 0.56, 0.32, 0.43, 2.04, 0.16, 0.14, 0.48, 0.18, 0.10, 0.57, 0.35, 0.08, 1.57, and 0.59. These scaling factors would be applied to mean mortality rates in 19 successive years of a simulation trial.

(3) I assume that a bad year for adult survival is also a bad year for foal survival, and vice versa. This makes sense if the major cause of year-to-year variation is the same for both foals and adults, e.g., winter weather conditions. This assumption is implemented by making the scaling factor for foal mortality perfectly correlated with that for adult mortality. The following formula is used to compute the value for foals:

$$f_{foal} = 1 + \frac{CV_{foal}}{CV_{ad}} (f_{ad} - 1)$$

where CV_{foal} and CV_{ad} are coefficients of variation of foal and adult mortality, respectively, and f_{foal} and f_{ad} are scaling factors for foal and adult mortality. This formula says that if the scaling factor for adults is, for example, 2 standard deviations above the mean, then it will be 2 standard deviations above the mean for foals also. For Pryor Mountain, a scaling factor for adult mortality of 4.4 would be 2 standard deviations above the mean scaling factor of 1.0, since SD for adults = 1.7 and $1.0 + 2 \times 1.7 = 4.4$. This would translate to a scaling factor of 5.0 for foals, since their SD = 2.0 and $1 + (2.0/1.7) \times (4.4-1) = 5.0$.

(4) Next, mortality is simulated for 24-year-old males to determine the number of 25-year-old males at the next census. This is repeated for 24-year-old females, then 23-year-olds, etc., all the way down to foals that survive to be yearlings. For each age class, the scaling factor described above is applied to the mean mortality rate to get an actual mortality rate for a given year of a given trial. For example, mean survival probability of 3-year-old males at Pryor Mountain is 0.965. This implies a mean mortality rate = $1 - 0.965 = 0.035$. If the scaling factor for the current year is 4.4, then actual mortality rate of 3-year-old males this year = $4.4 \times 0.035 = 0.154$. Mortality rates of all other age classes are adjusted similarly. This represents a moderately bad year. Conversely, if the scaling factor were 0.7, then mortality rate of 3-year-old males would be $0.7 \times 0.035 = 0.024$, indicating a better-than-average year for survival.

Once the actual mortality rate for an age/sex class in a given year of a given trial is calculated, the number of animals that survive to the next older age class is determined as follows. If the total number of horses in the age/sex class is less than 100, then a random number between 0 and 1 is picked for each animal, and that animal dies if the random

number is less than the actual mortality rate for its age class and lives otherwise.²

To continue the example from the previous paragraph, if the mortality rate of 3-year-old males in a given year of a given trial is 0.154 and there are 40 3-year-old males in the population, then the expected number of survivors to the next year is $(1-0.154) \times 40 = 33.84$. However, the actual number of survivors obviously has to be an integer -- it may be possible to have 0.84 of a horse, but unlikely that this partial horse would be alive! What the 0.154 mortality rate really means is that each horse has a probability = 0.154 of dying before the next census; the most realistic way to simulate this process is to have each individual horse either live or die according to probabilities of 0.846 and 0.154, respectively. This is called demographic stochasticity, in contrast with the unpredictable year-to-year variation in mortality rates, or environmental stochasticity, discussed above.

If the number of horses in a particular age/sex class exceeds 100, then the program would take too long to run if random numbers had to be picked for each individual animal. In this situation, either a normal or Poisson distribution is used to approximate the process of picking a random number for each individual and deciding whether that individual lives or dies based on whether the random number is above or below a cutoff value. If the cutoff value (i.e., mortality rate) is fairly low, then the Poisson is used because it is a better approximation than the normal; otherwise a normal approximation is used.

(5) Now surviving animals are one year older and we've progressed to the foaling season just before next year's census. Each age class has an effective foaling rate based on its mean foaling rate without management and any fertility control that has been applied in previous years. The foaling rate is further adjusted for year-to-year variation (environmental stochasticity) in the same manner as mortality rates were adjusted, but using the coefficient of variation of foaling rate instead of the CV for adult mortality or juvenile mortality. This means that year-to-year variation in foaling rate is uncorrelated with year-to-year variation in mortality. This reflects the situation at Pryor Mountain, although in other habitats a severe winter which caused increased mortality might also contribute to a reduced foaling rate the next summer.

The age-specific foaling rate adjusted to account for fertility control and environmental stochasticity is the probability that a female in each age class produces a foal. For each female in each age class, a random number between 0 and 1 is selected; if that number is less than the probability of having a foal, she does so (see footnote). The sex of that foal is determined similarly, based on the proportion of males among foals at birth. As described for mortality above, a normal or Poisson approximation is used if the number of females in an age class is large. Finally, the number of male and female foals produced by mothers of all ages are added up to give the total number of male and female foals produced in each year of each trial.

²To visualize this process, imagine a ruler 1 meter long. Divide the ruler into two segments with lengths determined by probabilities of living or dying. For example, if mortality rate is 0.1, then the portion of the ruler from 0 to 0.1 m would represent death and the proportion from 0.1 to 1.0 m would represent remaining alive. Picking a random number from 0 to 1 is equivalent to placing a mark at a random location on the ruler. If the mark is to the left of 0.1 (i.e., the random number is less than 0.1), the individual dies; otherwise it lives.

INTERPRETATION OF OUTPUT

The various kinds of output produced by the program have been described in the tutorial, and additional information about output is given in the on-line help screens. This section includes some miscellaneous notes about interpreting and manipulating output.

Population Trajectories

When you select **Run Simulation** from the Management Options menu, you will see how the population grows over time in each trial. Keep in mind that this shows the full management case only; i.e., with both fertility control and removal applied at the intervals determined by the schedule of gathers. If you want to see a similar "spaghetti graph" for an unmanaged population, try running a simulation without setting any options for fertility control or removal. The variation among trials results from both environmental and demographic stochasticity. If you set all coefficients of variation equal to zero, the variation seen on this graph will reflect only demographic stochasticity.

When viewing this graph, you may notice abrupt declines in population size at regular intervals. These result from removal of a fixed number of animals at each gather, or removals to reduce the population to a target size at each gather. If a fixed number which is a substantial proportion of the initial population size is removed fairly regularly, then there may be tremendous variation among population trajectories -- some going to extinction, others increasing rapidly.

I purposely designed the program so that this is the only output you are required to look at (all other output is optional), because this graph is a vivid demonstration of how random variation influences population growth. I think it's essential that wildlife managers become comfortable with the idea that precise, specific predictions of population trajectories are unrealistic.

Output for Specific Age/Sex Classes

For many of the graphs in the Output Results menu, you can display results for males, females, or both sexes and for foals, young animals (1 to 5 years old), older animals (> 5 years old), or all ages combined. We restricted age classes to these three, rather than permitting you to display results for any individual age (e.g., age 4), because of memory limitations of DOS-based computers. **Keep an eye on the settings of age class and sex to be displayed (in the box in the upper left of various output menu screens); if you change these, the changes are in effect for all subsequent displays until you change them again or exit the program.**

Saving Graphs and Tables to Disk

In addition to viewing and printing output, you can save both graphs and tables as disk files. For graphs, this might be useful if you were preparing a report and wanted to include a graph in the body of the report. Graphs are saved in PCX format, which can be imported into widely-used word-processing programs such as Word Perfect and Microsoft

Word. Tables are saved as ASCII (plain text) files, which can also be imported into a document by your word processor. If you wish to manipulate numerically results of this program, you can save a table as a disk file and then import it into a spreadsheet. For example, you might want to have this program compute cumulative numbers of removals and females treated under a particular management scheme, and then use your spreadsheet to calculate costs of removals and fertility treatment. Once you imported the table into your spreadsheet, you would use the *parse* procedure to break up each line of data into its individual values.

Computing Population Growth Rate

The program displays population sizes rather than population growth rates because growth rates may fluctuate markedly from year-to-year under intensive management. If you wish to compute average growth rates, the best way to do so is as follows:

- (1) Use the table showing Cumulative Distribution of Final Population Sizes.
- (2) For each final population size for the management case of concern, use this formula to compute average annual growth rate:

$$\text{growth rate} = \left(\frac{N_t}{N_0} \right)^{\frac{1}{t}}$$

where N_t = final population size, N_0 = initial population size, and t = number of years in the simulation. You will need to compute growth rate for each ending population size; the number of these equals the number of trials of the simulation. The initial population size is the same for each trial. This growth rate is the finite multiplication rate; i.e., the average factor by which the population is multiplied each year.

- (3) Compute the mean and standard deviation of these average growth rates.

It will probably save you time to automate these calculations in a spreadsheet.

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REFERENCES

(Items marked with an * are cited in the text.)

*Berger, J. 1986. Wild horses of the Great Basin: social competition and population size. University of Chicago Press, Chicago, IL, xxi + 326 pp.

Berger, J. 1991. Funding asymmetries for endangered species, feral animals, and livestock. *Bioscience* 41:105-106.

*Caswell, H. 1989. Matrix population models. Sinauer Associates, Inc., Sunderland, Massachusetts.

*Caughley, G. 1974. Interpretation of age ratios. *Journal of Wildlife Management* 38:557-562.

*Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, New York.

Choquenot, D. 1990. Rate of increase for populations of feral donkeys in northern Australia. *Journal of Mammalogy* 71:151-155.

Choquenot, D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. *Ecology* 72:805-813.

*Eagle, T. C., D. B. Siniff, J. R. Tester, R. A. Garrott, and E. D. Plotka. 1992. Efficacy of chemical contraception in feral mares. *Wildlife Society Bulletin* 20:211-216.

Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. *Journal of Wildlife Management* 49:997-1012.

*Eberhardt, L. L. 1988. Using age structure data from changing populations. *Journal of Applied Ecology* 25:373-378.

Eberhardt, L. L., A. K. Majorowicz, and J. A. Wilcox. 1982. Apparent rates of increase for two feral horse herds. *Journal of Wildlife Management* 46:367-374.

Freeland, W. J., and D. Choquenot. 1990. Determinants of herbivore carrying capacity: plants, nutrients, and *Equus asinus* in northern Australia. *Ecology* 71:589-597.

Garrott, R. A. 1991. Feral horse fertility control: potential and limitations. *Wildlife Society Bulletin* 19:52-58.

Garrott, R. A. 1991. Sex ratios and differential survival of feral horses. *Journal of Animal Ecology* 60:929-936.

*Garrott, R. A. 1991. Bias in aging feral horses. *Journal of Range Management* **44**:611-613.

*Garrott, R. A., T. C. Eagle, and E. D. Plotka. 1991. Age-specific reproduction in feral horses. *Canadian Journal of Zoology* **69**:738-743.

Garrott, R. A., and D. B. Siniff. 1992. Limitations of male-oriented contraception for controlling feral horse populations. *Journal of Wildlife Management* **56**:456-464.

Garrott, R. A., D. B. Siniff, and L. L. Eberhardt. 1991. Growth rates of feral horse populations. *Journal of Wildlife Management* **55**:641-648.

*Garrott, R. A., D. B. Siniff, J. R. Tester, T. C. Eagle, and E. D. Plotka. 1992. A comparison of contraceptive technologies for feral horse management. *Wildlife Society Bulletin* **20**:318-326.

*Garrott, R. A., and L. Taylor. 1990. Dynamics of a feral horse population in Montana. *Journal of Wildlife Management* **54**:603-612.

Groenendaal, J. V., H. De Kroon, and H. Caswell. 1988. Projection matrices in population biology. *Trends in Ecology & Evolution* **3**:264-269.

*Jenkins, S. H. 1989. Comments on an inappropriate population model for feral burros. *Journal of Mammalogy* **70**:667-670.

*Keiper, R., and K. Houpt. 1984. Reproduction in feral horses: an eight-year study. *American Journal of Veterinary Research* **45**:991-995.

*Kirkpatrick, J. F., I. K. M. Liu, and J. W. Turner Jr. 1990. Remotely delivered immunocontraception in feral horses. *Wildlife Society Bulletin* **18**:326-330.

*Kirkpatrick, J. F., and J. W. Turner, Jr. 1991. Compensatory reproduction in feral horses. *Journal of Wildlife Management* **55**:649-652.

Lebreton, J. D., R. Pradel, and J. Clobert. 1993. The statistical analysis of survival in animal populations. *Trends in Ecology & Evolution* **8**:91-95.

*Liu, I. K. M., M. Bernoco, and M. Feldman. 1989. Contraception in mares heteroimmunized with pig zonae pellucidae. *Journal of Reproduction and Fertility* **85**:19-29.

Noon, B. R., and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis. Pages 441-464 *in* D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001: Populations*. Elsevier Applied Science, London, England.

Perryman, P., and A. Muchlinski. 1987. Population dynamics of feral burros at the Naval Weapons Center, China Lake, California. *Journal of Mammalogy* **68**:435-438. (Don't read this without also reading Jenkins [1989].)

*Plotka, E. D., D. N. Vevea, T. C. Eagle, J. R. Tester, and D. B. Siniff. 1992. Hormonal contraception of feral mares with silastic rods. *Journal of Wildlife Diseases* 28:255-262.

*Turner, J. W., Jr., and J. F. Kirkpatrick. 1991. New developments in feral horse contraception and their potential application to wildlife. *Wildlife Society Bulletin* 19:350-359.

Turner, J. W., Jr., M. L. Wolfe, and J. F. Kirkpatrick. 1992. Seasonal mountain lion predation on a feral horse population. *Canadian Journal of Zoology* 70:929-934.

Wolfe, M. L. 1980. Feral horse demography: a preliminary report. *Journal of Range Management* 33:354-360.

*Wolfe, M. L., L. C. Ellis, and R. Macmullen. 1989. Reproductive rates of feral horses and burros. *Journal of Wildlife Management* 53:916-924.

