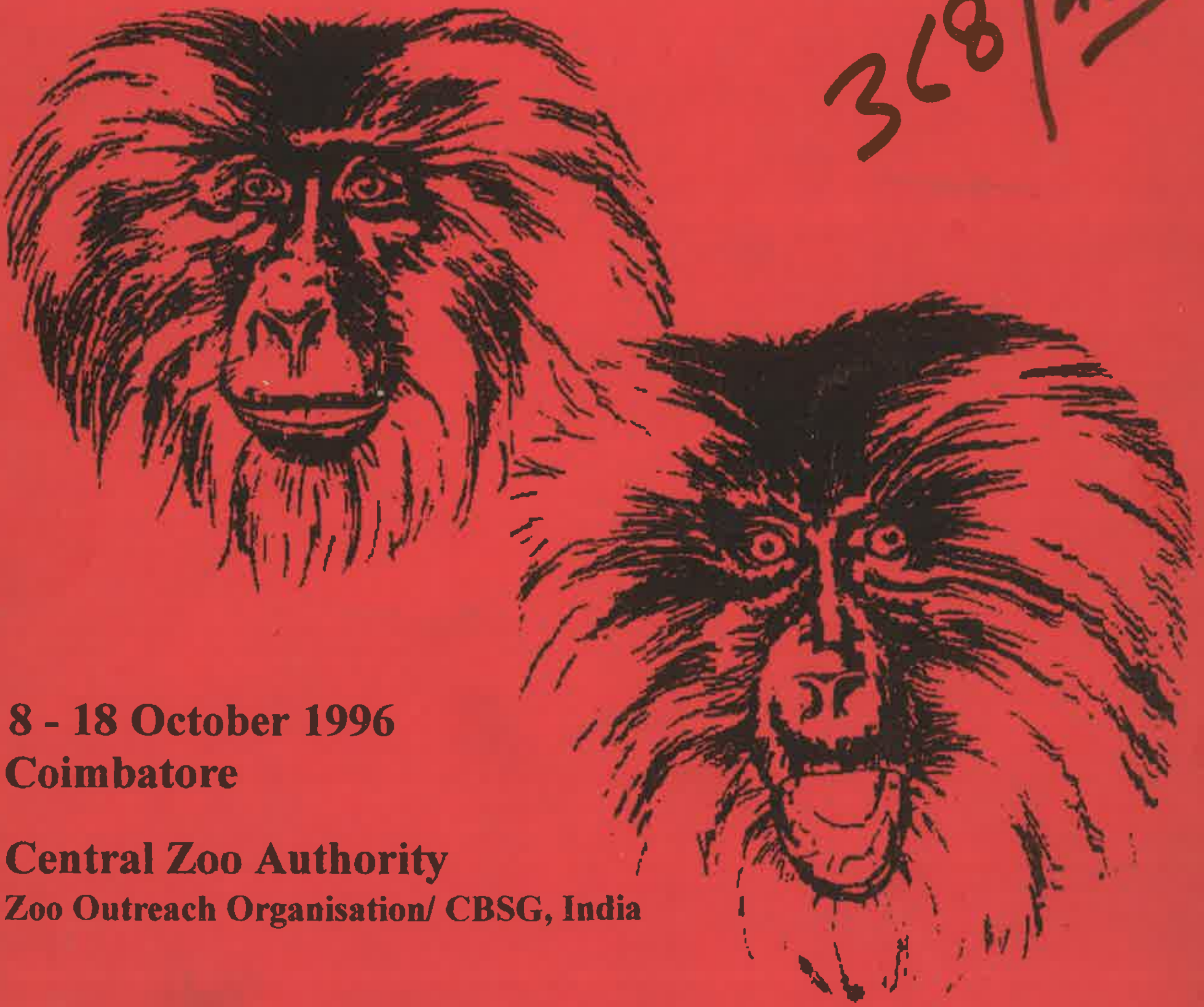
VORTEX :

Population Modelling
-- with L. T. M. Case Study

Small Population Dynamics and the Tools of Recovery Training Workshop



8 - 18 October 1996
Coimbatore

Central Zoo Authority
Zoo Outreach Organisation/ CBSG, India

VORTEX : Population Modelling -- with LTM Case Study

Briefing Book

for the Training Workshop
Small Population Dynamics and the Tools of Recovery with LTM Case Study

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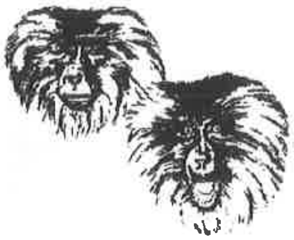

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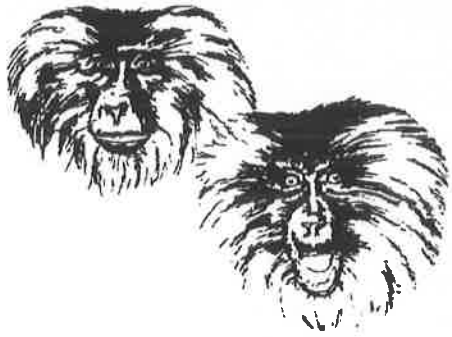

Small Population Dynamics
and Tools of Recovery Training Workshop
6 - 18 October 1996, Coimbatore

Contents

VORTEX

A Stochastic Simulation of the Extinction Process

Version 7

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Additional copies of *VORTEX Version 7 User's Manual* can be ordered through the IUCN/SSC Conservation Breeding Specialist Group, 12101 Johnny Cake Ridge Road, Apple Valley, MN, 55124, USA.
Send checks for US $35.00 (for printing and shipping costs) payable to CBSG; checks must be drawn on a US bank. Funds may be wired to First Bank NA ABA No. 091000022, for credit to CBSG Account No. 1100 1210 1736.

VORTEX

A Stochastic Simulation of the Extinction Process

Version 7

Chapter I:

User's Reference

CONTENTS

WHAT'S NEW IN VERSION 7

- Files included on the distribution disk, to be copied to the working directory of the hard disk, are:

  vortex.exe
  dos4gw.exe
  dos4gw.doc
  pminfo.exe
  rminfo.exe
  vortex.doc
  vortexx.exe
  vortgraf.exe

  Only vortex.exe and dos4gw.exe are needed to run the program, but the other files may be useful to some people.

- The screen will appear to freeze on input if the value that is entered is impossible. Read the prompt at the bottom of the screen for help with the acceptable range. Re-enter a value within that range. VORTEX rejects values that are impossible (those that would cause the system to crash); it will accept mathematically possible, but biologically implausible, input values.

- Size of analysis now has absolute limits of:

30 000	initial animals (including supplements)
60 000	carrying capacity (maximum in good years of EV)
60 000	population size (following reproduction, in best years, at maximum K)
100	types of catastrophes
250	maximum age
100	maximum litter size
20	populations
10 000	years simulated
10 000	iterations

  The amount of RAM on the system will almost certainly impose stricter limits on the analysis. Presently, VORTEX can access up to 32 MB of RAM; future versions will likely be able to use up to 4 GB of RAM.

  Note: VORTEX can handle analyses of populations that are much larger than is reasonable to model with VORTEX. Populations larger than a few 1000s will run very slowly and, more importantly, the types of stochasticity modeled well by VORTEX (demographic and genetic) are largely irrelevant to such populations. Other PVA models (e.g., RAMAS) are probably more appropriate in those cases.

- VORTEX is now compiled with the Watcom C386 compiler. Version 7 can run only on 80386 and more advanced computers. You must have the DOS extender DOS4GW.EXE (supplied) in the directory in order to run VORTEX. To analyze large populations, the program will use either expanded or extended memory. If you have problems with a lack of memory, configure your computer to maximize the amount of expanded (e.g., EMM386 or QEMM386) memory. VORTEX, as presently configured, can use up to 32 MB of expanded memory for the analyses. Two utility programs, RMINFO and PMINFO are provided so that the very knowledgeable users can determine the amount and kind of memory that will be used by the DOS4GW memory manager. VORTEXX is provided to allow use of the program on older (8086, 80286) computers, but with slower performance and the loss of the ability to access extended memory.

If you have problems with exceedingly slow analyses:

i. Don't use the Heterosis option for inbreeding depression. It requires a lot of memory and can slow the program tremendously.
ii. Buy a faster computer (e.g., 80486 or Pentium or P6 or ...).
iii. Do a smaller analysis. Often a large population (or meta-population) may exist, but the real concern is whether small fragments of the population will survive. VORTEX will simulate small populations much more rapidly than large populations or constellations of populations within a meta-population. If local populations don't exchange migrants, analyze them separately rather than as parts of a meta-population.
iv. Use a different program. If your analyses are exceedingly slow, then the population being analyzed is probably so large that the kinds of stochastic forces (e.g., demographic stochasticity, inbreeding) modeled well by VORTEX are unlikely to be relevant to the population dynamics. It may be more appropriate to use a simulation, such as RAMAS, that is not individual-based, or use analytical methods (e.g., life table analysis) that exclude stochastic factors entirely.

- VORTEX now gives the user the option of crudely displaying population size changes on the screen as the program runs. This is a good way to see what is happening, during testing and exploratory analyses, but it will moderately slow the analyses. The screen display of population sizes can be toggled on/off with the F2 key.

- If the user chooses to produce files of data for later plotting, VORTEX will go to a screen graphics option after the analysis is completed. The user then has the option of displaying graphs of various output parameters for any analyses that have been run with the graphics files option invoked (i.e., any data sets in the VORTEX.DAT file created by VORTEX). This option for screen graphs is disabled if the input data were provided in a file (as opposed to keyboard input), as it is assumed that the analysis will be run unattended.

- VORTEX now allows modeling of hermaphroditic species, in which each organism can mate with any other individual. All individuals are labelled female in this option. The user can specify the rate of selfing that occurs.

- VORTEX now allows the user to specify that individuals migrating between populations suffer additional mortality.

- Several changes were made to facilitate the generation of multiple scenarios to be tested. VORTEX will now accept a file of input data as the default values to be used when input parameters are to be entered from the keyboard. If no input file is available or desired for the defaults, then VORTEX will (as before) generate its own default values. When multiple scenarios are entered from the keyboard, the default values for each new scenario to be simulated are taken from the previous scenario.

More changes are likely in the future. Notification of upgrades will be sent to anyone known by the CBSG (12101 Johnny Cake Ridge Road, Apple Valley, MN 55124 USA; phone (612) 431-9325; fax (612) 432-2757) to be a user.

VORTEX - A Stochastic Simulation of the Extinction Process
Version 7

The VORTEX program is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wildlife populations. VORTEX models population dynamics as discrete, sequential events (e.g., births, deaths, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or as random variables that follow specified distributions.

VORTEX simulates a population by stepping through the series of events that describe the typical life cycle of sexually reproducing, diploid organisms. The program was written originally to model mammalian and avian populations, but it has been used for modeling some reptiles and amphibians and perhaps could be used for fish, invertebrates, or even plants -- if they have relatively low fecundity or could be modelled as if they do. The simulation of the population can then be repeated to reveal the distribution of fates that the population might experience.

The purpose of this manual is to provide instructions on how to install and use VORTEX. It is not intended as a primer for small population biology; you must be conversant with this discipline to use VORTEX appropriately. However, Chapter 2 of this manual gives a brief introduction to small population biology. Chapter 3 is a pre-print of a paper describing more generally the use of Population Viability Analysis to assist with wildlife management and endangered species recovery. Chapter 5 is a sort of technical reference, and reprints a paper from *Wildlife Research* which describes the assumptions, algorithms, and uses of VORTEX in more detail. In addition, a number of references are provided in Chapters 4 and 5. We urge you to read the entire User's Manual not only to better your understanding of VORTEX, but to enhance your appreciation of the perils facing small populations. Starfield and Bleloch (1986) and Burgman et al. (1993) provide very good introductions to population modeling.

In addition, you must know the biology of the species which you intend to model. You should gather as much information as possible for VORTEX simulations to be meaningful. The old computer adage of "garbage in, garbage out" is aptly applied to VORTEX. However, many questions asked by VORTEX cannot be answered simply because the data do not exist. The only recourse that you will have is to enter your best guess. Oftentimes, your best guess is not yours alone. Most (if not all) Population Viability Analyses (PVA) have succeeded through the efforts of many. Two or more heads are usually better than one when you find yourself faced with a VORTEX question with no known answer. Default values are provided by VORTEX to indicate plausible values for each parameter; the defaults were not selected to model the population biology of any particular species.

Thus, the fundamental processes involved to insure success are to read the manual, muster information on the species of interest, and gather your colleagues.

GETTING STARTED

VORTEX is written in the C programming language. VORTEX is compiled for use on microcomputers using the MS-DOS operating system. A version for Macintosh™ computers is also available (see page 48 for notes on the Macintosh version). VORTEX (MS-DOS version) can be operated on computers having the following specifications:

Central Processor: Intel 80386, 80486, or Pentium. VORTEX will not run on older CPUs (i.e., 8088, 8086, 80286), but a version of the program, VORTEXX, is provided for those users who do not have access to more powerful PCs.

Math Coprocessor: Highly desirable, but not mandatory. A math coprocessor can increase computation speed by as much as fivefold.

Random Access Memory (RAM): A minimum of 640K installed RAM is required. VORTEX can utilize extended or expanded memory if it is available (see later).

Video Card: VORTEX supports any CGA/VGA/EGA video card.

Monitor: The monitor screen must be able to display 80 characters wide and 25 lines deep; this may eliminate the use of some laptop computers.

INSTALLATION

VORTEX is provided on 3.5", double-sided, high-density disks (1.44 MB capacity). VORTEX is also available on double density (720 KB) or 5.25" disks on special order only. VORTEX is not copy protected. You may make as many copies as you wish, and we advise that you make at least a backup disk copy of the VORTEX programs. Although nothing prevents nor even discourages you from giving copies to other people with a need for the program, only users who are known to the IUCN SSC Conservation Breeding Specialist Group will receive notices of updates, error reports, and other important information. (Unauthorized *sale* of the program or manual in any form constitutes violation of copyright laws.) All users are encouraged to notify the CBSG of their interest in and use of VORTEX.

Installing VORTEX on a Hard Drive

Place your VORTEX floppy disk into your computer's floppy drive. On most computers, this floppy drive is designated as “A”, while the hard disk drive is designated as “C”. This convention will be used throughout the following instructions. If your drive designations are different, merely substitute the appropriate designation. For example, some computer's 3.5" floppy disk drive is designated as “B” instead of “A”.

Also, we will use the convention of calling the "Return" or "Enter" key simply **Enter**. Another convention will be the use of **`bold face`** to indicate exactly which letters or numerals we wish you to type for a given command or entry. For example, the following instruction:

```
C:\>DIR A: (Enter)
```

means that you are *only* to type **`DIR A:`** after the "C prompt" (`C:\>`) and then enter this command by pressing the **Return** or **Enter** key.

Your VORTEX disk should contain the following files:

- VORTEX.EXE
- VORTEX.DOC
- DOS4GW.EXE
- DOS4GW.DOC
- RMINFO.EXE
- PMINFO.EXE
- VORTEXX.EXE
- VORTGRAF.EXE

You must have both the VORTEX program (VORTEX.EXE) and the DOS extender DOS4GW.EXE in the directory in order to run VORTEX. The *.DOC files on the distribution disk provide some information about these programs. RMINFO.EXE and PMINFO.EXE are programs that analyze the memory configuration of the computer and report how the program DOS4GW will access and use extended memory. (You need to worry about memory usage only if you are having trouble and if you are knowledgeable about memory configurations.)

VORTEXX is a version of the program which can run on computers with 8086 or 80286 processors. VORTEXX cannot use extended or expanded memory (thereby considerably limiting the size of population that can be analyzed), and it does not provide graphical display of results. If for any reason you cannot get VORTEX to run on your machine, you might try VORTEXX. VORTGRAF is a program which will display results from previous VORTEX analyses as graphs on the screen.

To install VORTEX on your computer's hard disk drive, you should first create a directory where the program will reside. To do this, type the following after the prompt:

```
C:\>MD \VORTEX (Enter)
```

To copy the VORTEX programs and files onto your hard disk drive, insert the floppy disk containing the VORTEX program into your "A" floppy disk drive. Then, enter the following command after the prompt:

```
C:\>COPY A:*.* C:\VORTEX (Enter)
```

EXTENDED AND EXPANDED MEMORY (memory above I MB)

For analyses that use the Heterosis Inbreeding Depression option (see later), VORTEX can require large amounts of computer memory. In such cases, VORTEX can make use of any extended memory (including XMS) or expanded memory (e.g., memory managed by EMM386 or QEMM) available on your computer. Extended or expanded memory will be necessary to run analyses with the Heterosis Inbreeding Depression option on populations of greater than about 300 animals. Without the Heterosis option, substantially more animals can be analyzed with any given memory available. VORTEX does not *need* extended memory to operate, and it will not operate any faster with extended memory, but it does allow you to analyze larger populations.

To check existing memory manager programs and available memory, run the MS-DOS program MEM by typing the following:

```
C:\>MEM/C |MORE (Enter)
```

Note the use of the MORE switch following the "pipe" symbol (" | "). This prevents the display from scrolling off the top of the screen.

[Note: Earlier versions of VORTEX used the EX286 memory manager to access extended memory. The programs EX286 and TUNE which were provided with VORTEX Version 5 should not be used with Version 7.]

VORTEX, as presently configured, can use up to 32 MB of expanded memory for the analyses. Two utility programs, RMINFO and PMINFO are provided so that the more knowledgeable users can determine the amount and kind of memory that will be used by the DOS4GW memory manager.

LIMITATIONS ON THE SIZE OF THE ANALYSIS

VORTEX allocates memory as it needs it, and will try to make optimal use of the memory in your computer to carry out the analyses. VORTEX places the following absolute limits on the size of analyses:

30 000	initial animals (including supplements)
60 000	carrying capacity (maximum in good years of environmental variation)
60 000	population size (following reproduction, in best years, at max. K)
100	types of catastrophes
250	maximum age
100	maximum litter size
20	populations
10 000	years simulated
10 000	iterations

The amount of RAM on the system will almost certainly impose stricter limits on the analysis. Presently, VORTEX can access up to 32 MB of RAM; future versions will likely be able to use up to 4 GB of RAM.

Some combinations of parameters (for example, particularly large litter sizes with large fluctuations in carrying capacity) can require large amounts of memory, however, and VORTEX will abort the analysis if memory is insufficient. The Heterosis Inbreeding Depression option requires especially large amounts of computer memory (more than 25 MB of extended or expanded memory will be needed to analyze a population that reaches 5 000 living animals!) and computer time.

If you have problems with exceedingly slow analyses:

- don't use the Heterosis option for inbreeding depression. It requires a lot of memory and can slow the program tremendously.
- buy a faster computer (e.g., 80486 or Pentium or P6 or ...).
- do a smaller analysis. Often a large population (or meta-population) may exist, but the real concern is whether small fragments of the population will survive. VORTEX will simulate small populations much more rapidly than large populations or constellations of populations within a meta-population. If local populations don't exchange migrants, analyze them separately rather than as parts of a meta-population.
- use a different program. If your analyses are exceedingly slow, then the population being analyzed is probably so large that the kinds of stochastic forces (e.g., demographic stochasticity, inbreeding) modeled well by VORTEX are likely to be irrelevant to the population dynamics. It may be more appropriate to use a simulation, such as RAMAS/Space (Applied Biomathematics, Setauket, NY), that is not individual-based, or use analytical methods (e.g., life table analysis) that exclude stochastic factors entirely.

STARTING VORTEX

To run the VORTEX program, make sure that you are in the VORTEX directory (or wherever you placed the files VORTEX.EXE and DOS4GW.EXE), and then type:

```
C:\VORTEX>VORTEX (Enter)
```

VORTEX goes through the simulation process by asking several questions. Each of these questions will be explained briefly in this manual. A more thorough explanation of the rationale behind most of the questions and algorithms can be found in the *Wildlife Research* manuscript reprinted as Chapter 5 of this manual.

QUITTING VORTEX

To quit VORTEX at any time press the **F1** key or the "Control" and "C" (or the "Control" and "Break") keys simultaneously.

DATA INPUT

VORTEX will accept just about any input that you provide. The data entry screen will appear to freeze on input if the value entered is impossible. Read the prompt at the bottom of the screen for help with acceptable range. Re-enter a value within that range. VORTEX rejects values that are impossible (those that would cause the system to crash); it will accept mathematically possible, but biologically implausible, input values.

VORTEX does provide some instructions at the bottom of the screen for most questions, such as whether to enter the answer as a decimal or as a percent. But the responsibility for entering valid data rests with you. VORTEX does create ASCII files that can be edited. These files contain all the input data and are created as soon as data entry is completed. This provides you with an opportunity to correct specific input errors without having to enter all the data over again. These files will be explained near the end of this manual.

VORTEX's questions will have answers already provided; these are called *default answers* or *default values*. To accept these values without change, simply press the **Enter** key or the DOWN CURSOR (↓). Otherwise, type over the default answer with your value. Questions requiring a "Yes" or "No" answer can be answered by accepting the default response, or by entering `Y` for Yes or `N` for No. (VORTEX is insensitive to the case of input, so `y` or `n` would work as well.) Some data entry points will expand into "subwindows" when the cursor is moved to that position. Additional information and questions will then become available. You can move between lines of input data by using the cursor keys (↓ and ↑).

You can test VORTEX (and see what it does) by simply accepting all the default values and letting the simulation run. The defaults model a metapopulation for which the deterministic population growth rate is 0%, that is, zero population growth would be expected based on the mean birth and death rates. The default population is so small, however, that it fluctuates considerably in size and is unstable because of stochastic (random) processes.

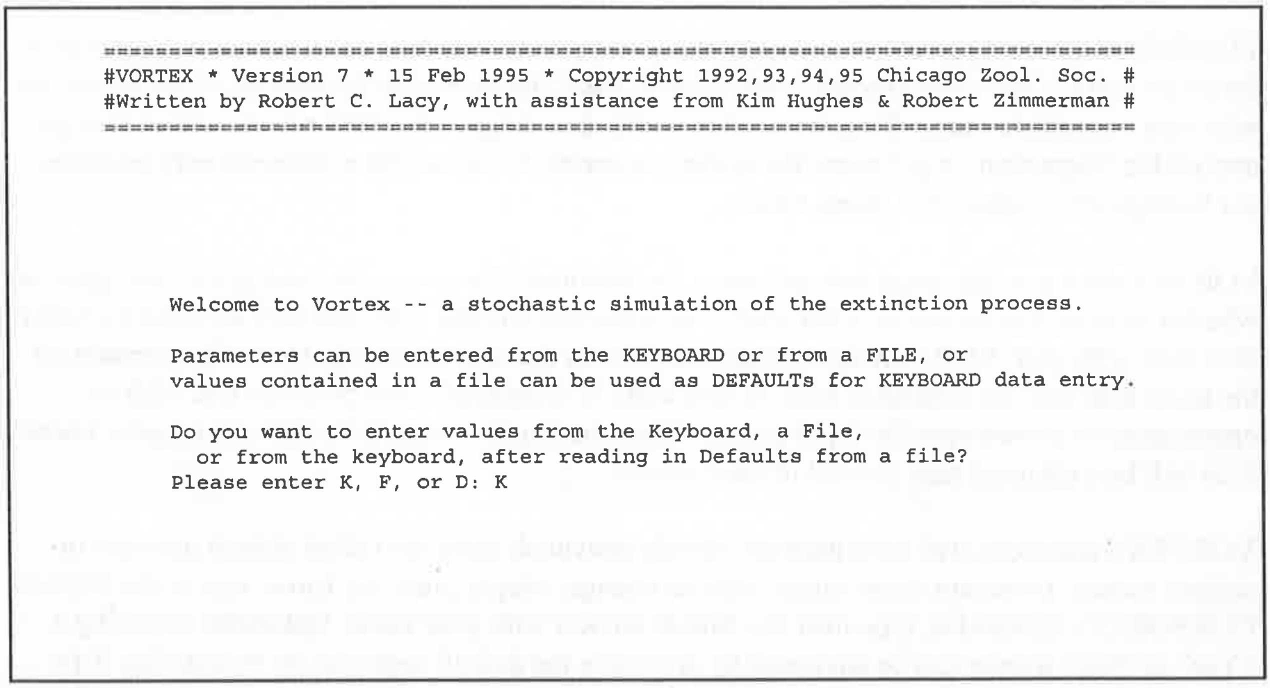
When VORTEX begins, you will be asked,

```
Do you want to enter values from the Keyboard, a File,
  or from the keyboard, after reading in Defaults from a file?
```

(Figure 1-1)

Entering data from the keyboard creates an *input file* that can be used later in subsequent analyses with modifications, if desired. Therefore if this is the *first time* you have used

VORTEX, no input file will have been previously created and your only response to this question is `K`, the default value. If you have previously entered data, and thereby created an input file, you can choose either to run the analysis with the input values from the file (by typing `F`), or to read in the values from the file as the defaults to be used as you enter data from the keyboard (by typing `D`).



```
==============================================================================
#VORTEX * Version 7 * 15 Feb 1995 * Copyright 1992,93,94,95 Chicago Zool. Soc. #
#Written by Robert C. Lacy, with assistance from Kim Hughes & Robert Zimmerman #
==============================================================================




     Welcome to Vortex -- a stochastic simulation of the extinction process.

     Parameters can be entered from the KEYBOARD or from a FILE, or
     values contained in a file can be used as DEFAULTs for KEYBOARD data entry.

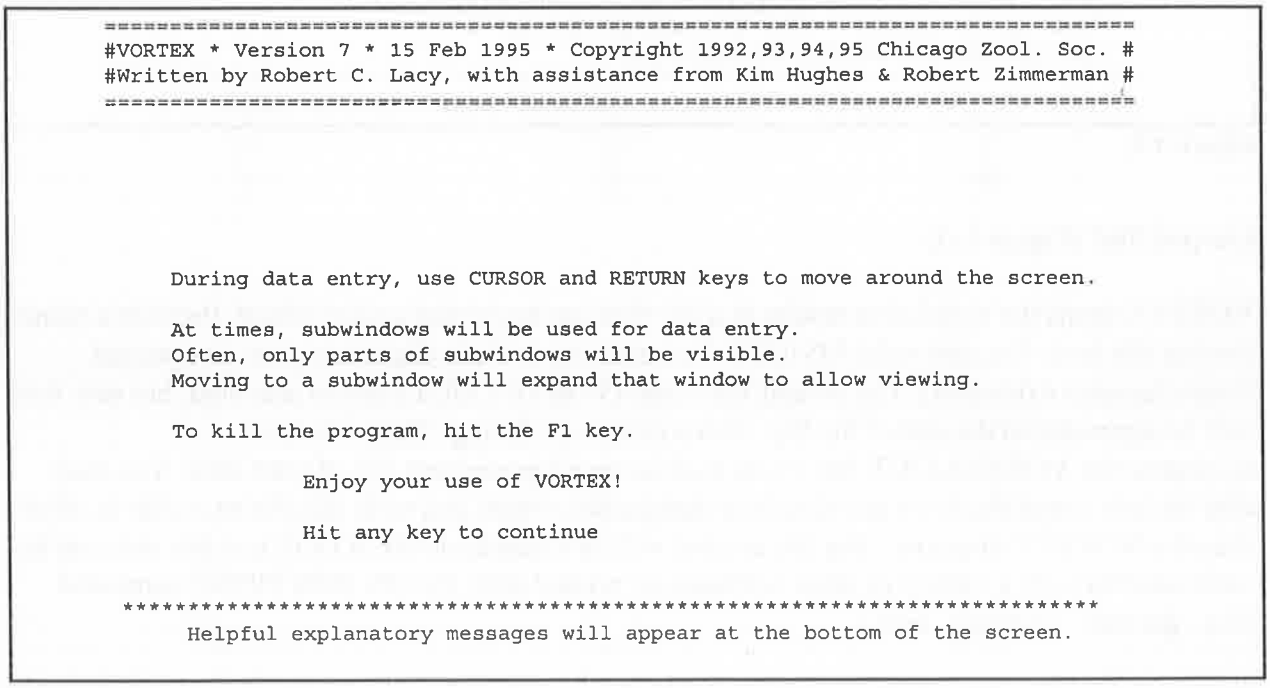
     Do you want to enter values from the Keyboard, a File,
       or from the keyboard, after reading in Defaults from a file?
     Please enter K, F, or D: K
```

Figure 1-1.

The input file created automatically when you enter input from the keyboard will be named VORTEX.IN. You can change it to some other name with the MS-DOS copy command (e.g., **`copy vortex.in myfile.in`**) or rename command (e.g., **`rename vortex.in myfile.in`**). Naming it in a way that identifies the case you were modeling can be useful. Each time VORTEX is started and data entered from the keyboard, VORTEX will destroy any existing file named VORTEX.IN and create a new input file from the current input. Thus, if you wish to save an input file, it is important that you rename or copy it to another file name before you next run VORTEX. After an input file is safely renamed or copied, you may wish to change a few input parameters and then re-run the analysis. In this way, you can test the sensitivity of the simulation results to changes in certain parameters. (You can also, of course, fix input data that was entered incorrectly the first time.) The VORTEX.IN file contains a vertical list of input values with labels. (The labels are there to help you; VORTEX ignores them.) Leave at least one space between the data and the labels. Editing input files can be done with any text editor (e.g., the MS-DOS Edit command), but beware that if you edit the input file with most word processors, you will have to save it as a DOS text file for it to be readable by VORTEX.

Unless you are a seasoned VORTEX user, it can be difficult to make even seemingly simple changes to the input data file. This is because the input parameters requested by VORTEX often depend on the answers given to other questions. Thus, a change in one answer can necessitate changes in many other parameters -- just to get VORTEX to run. An easier way to change some values in an input file is to ask VORTEX to use the old input file as the default parameters (option **D**), to be modified with further keyboard entries. When this is done, VORTEX will create a new data file (called VORTEX.IN) with the adjusted input values. (It will also run the analysis with the new input values.)

If you entered **K** for keyboard entry, you will next see a screen (Figure 1-2) providing brief instructions on data entry. If you entered **D** or **F**, you will be asked to provide the name of the input file to be read. The following explanations of data entry assume that you are entering data from the keyboard.



```
=============================================================================
#VORTEX * Version 7 * 15 Feb 1995 * Copyright 1992,93,94,95 Chicago Zool. Soc. #
#Written by Robert C. Lacy, with assistance from Kim Hughes & Robert Zimmerman #
=============================================================================




     During data entry, use CURSOR and RETURN keys to move around the screen.

     At times, subwindows will be used for data entry.
     Often, only parts of subwindows will be visible.
     Moving to a subwindow will expand that window to allow viewing.

     To kill the program, hit the F1 key.

               Enjoy your use of VORTEX!

               Hit any key to continue

 ***************************************************************************
      Helpful explanatory messages will appear at the bottom of the screen.
```

Figure 1-2.

Press any key to continue with the program.

You will now begin answering a series of questions that will create the data file that will be used in the simulation process. Each question or desired data entry will be presented below with an explanation of the information sought.

```
     Output file? VORT.100
+-------------------------------------------------------------------------------+
|    Do you want data files produced for graphing? Y                            |
|    Data from every iteration (Y), or means across iterations (N)? N           |
|    Do you want display of population sizes during iterations? Y               |
+-------------------------------------------------------------------------------+
     At what time interval do you want extinction reports? 10
     How many populations do you want to model? 2
+-------------------------------------------------------------------------------+
|    Enter youngest age to migrate:1                                            |
+-------------------------------------------------------------------------------+
+-------------------------------------------------------------------------------+
|    Do you want to incorporate inbreeding depression? Y                        |
+-------------------------------------------------------------------------------+
     Do you want EV(reproduction) to be correlated with EV(survival)? Y
     How many types of catastrophes do you want to model? 2
     Monogamous (M), polygynous (P), or hermaphroditic (H)? P
     At what age do females normally begin breeding? 2
     At what age do males normally begin breeding? 2
     What is the maximum age, beyond which all animals die? 10
     What is the sex ratio (proportion males) at birth? 0.500
     What is the maximum number of young per litter? 2
     Is reproduction density dependent? N
 ****************************************************************************
     Data for graphing will be placed in VORTEX.DAT and NVORTEX.DAT files.
```

Figure 1-3.

Output file? (Figure 1-3)

VORTEX sends the simulation results to a file that can be printed and/or edited. Provide a name for that file here. Use any valid MS-DOS file name (up to eight characters plus an optional three-character extension). The default file name (VORTEX.OUT) can be accepted, but new data will be appended to the end of the file, which can be confusing. Thus, it is best to rename the VORTEX.OUT file if you wish to save a permanent file of your own. You may also include a specific drive and directory designation where you wish this file to reside in other than the VORTEX directory. The file created will be a standard ASCII DOS text file that can be addressed through a variety of other software, or printed with the MS-DOS PRINT command (e.g., `print vortex.out`).

Do you want data files produced for graphing?

VORTEX can produce a file listing a number of output statistics, such as population size, probability of extinction, and measures of genetic diversity. These data will be placed in ASCII text files named VORTEX.DAT and (optionally) NVORTEX.DAT that can later be used as input to graphics or statistics software. If you want to create files for graphing or other analyses, enter `Y`. If you request data files for graphing, after the simulation is complete VORTEX will provide the option of seeing graphs of population size, gene diversity (expected heterozygosity), inbreeding, probability of extinction per time interval, and probability of population persistence. The graphs are shown on the screen, but you can capture the images with other software (e.g., the

GRAB command in WordPerfect) that will allow printing of the graphs. The screen graphs option is disabled is data are input via a file, rather than the keyboard, as it is assumed that the analysis will run unattended. A program, VORTGRAF, is provided to allow you to display graphical output from previous analyses without having to re-enter VORTEX and complete another simulation.

If you chose to produce data files for graphing, you will next be asked the following:

Data from every iteration (Y) or means across iterations (N)?

If you want data from each simulation plotted, enter `Y`. The results will be a file (NVORTEX.DAT) that gives the changes in population size for each simulation. If many (say, 100) simulations are run for many (say, 100) years, this file can be quite large (10 000 lines of numbers in the above case). Entering `N` will produce only a data file, named VORTEX.DAT, with output values averaged across iterations, and with standard errors of means across iterations.

Do you want display of population sizes during iterations?

VORTEX can display the changing population sizes during the simulation. The displays of population size are rather coarse—with a resolution of only 20 increments—and they usually go by so fast that they are hard to read. These crude graphics do, however, provide a nice way to visualize the approximate behavior of the population, while the simulations are being done. If you are modeling a meta-population consisting of multiple populations, the screen display will show the population sizes of the meta-population and of each component population. Each iteration adds new data points to the screen, so the display rapidly becomes unreadable. At any time during the simulation, you can clear the screen of all previous iterations by pressing the **F3** key. Because it takes computer time to plot the population sizes on the screen, the screen display will slow down the simulation. The screen graphics can be toggled off/on at any time during the simulation by pressing the **F2** key. If you do not plan to stare at the screen as the analysis is running, it makes sense to toggle off the display of population sizes, or to have specified (answer `N`) that you did not want to see the display of population size changes.

How many times do you want the simulation repeated?

The answer to this question tells VORTEX how many times (“runs” or “iterations”) you wish to repeat the simulation, given the data that you will provide in the subsequent steps. Because VORTEX uses a random number generator to simulate random events in the life cycle, no two iterations will be identical. Thus, to obtain a better "picture" of your data, you will want multiple iterations of your data. To see if your input parameters are appropriate, you may wish to limit the number of runs to 10. If you wish to obtain a crude picture of your results, enter 100. Once you are confident of your input data, 1,000 iterations are not excessive!

How many years do you want the simulation to run?

How far into the future do you wish to project your population? The usual answer to this question is 100-200 years, although fewer years can be input in order to assess input parameters, or to examine the short-term viability of a population. If you simulate populations for just a few decades, however, you should be aware that processes controlling population dynamics might be leading the population toward extinction but, especially for long-lived species, the final extinction may not occur for fifty or more years. By the time that the factors causing extinction are apparent, the extinction process might be so far along as to be almost irreversible. (One of the big advantages of PVA modeling is that it can reveal the instability of a population long before it would be obvious in the field.)

An important point to remember is that VORTEX does not necessarily consider "years" as calendar years. Rather, VORTEX considers years as "time cycles". If the species that you are modeling is short-lived (mice or shrews, for example), then the use of true calendar years would be inappropriate to model the birth and death dynamics. A "year" for short-lived species may actually represent only one or a few months. Remember to be consistent with whatever time cycle that you define as a year when entering parameters (such as birth and death rates and probabilities of catastrophes).

At what time interval do you want extinction reports?

The answer to this question defines how often you wish to see summary data regarding population size, probability of extinction, and measures of genetic variance. Most users answer 5 or 10 years, depending on the length of the simulation. For example, if you are using simulations of 100 years, an interval of 10 years should be satisfactory. You may obtain extinction reports for each year by entering `1`.

How many populations do you want to model?

VORTEX can model single populations or metapopulations. See Chapter 2 for a discussion of metapopulation theory. The maximum number of populations that you can model is 20. Keep in mind that metapopulation analysis runs much slower than single population modeling. If there isn't an opportunity for exchange of migrants among populations in your model, it would be faster to run several individual simulations (each one modeling an isolated population) instead of the metapopulation model.

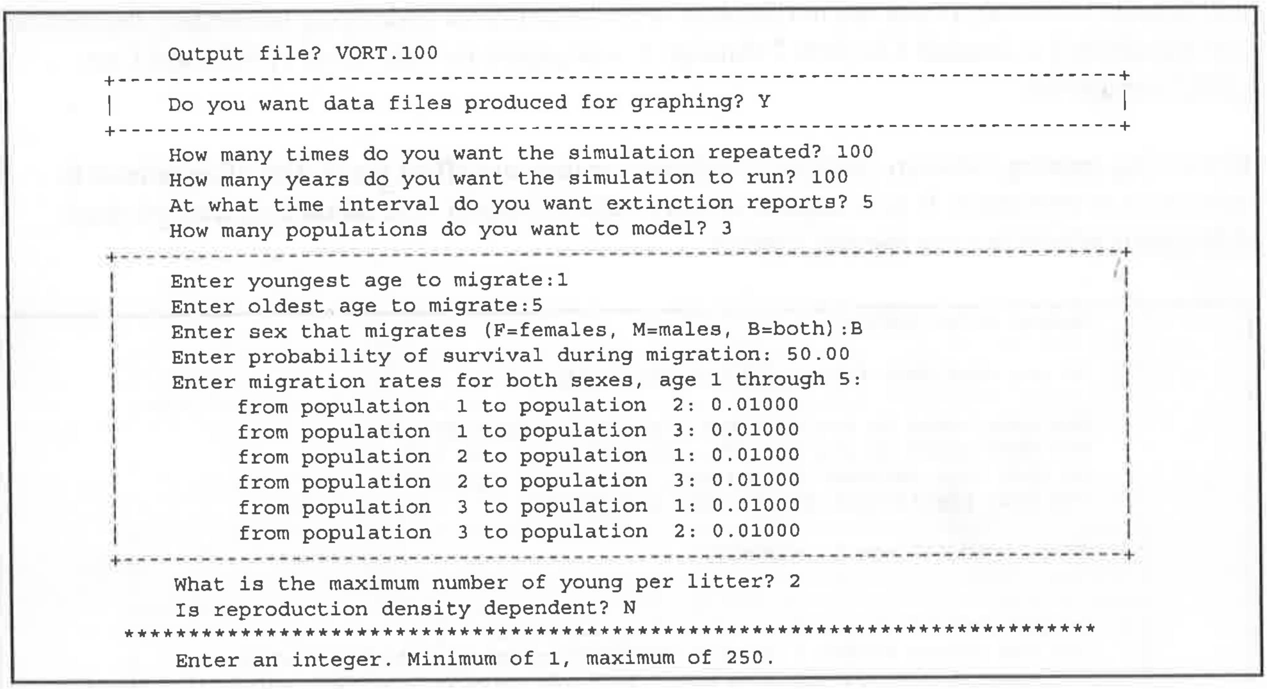
Enter the number of populations that depicts your metapopulation model or enter `1` for a single population simulation. If you enter a number greater than one, you will see the next set of five questions; otherwise the questions in the migration input window will be skipped.

Enter youngest age to migrate: (Figure 1-4)

If you have chosen the metapopulation model (entering a number greater than 1 above), you must define the migration rates among all the populations, and you must specify which sex(es) and age(s) migrate. Enter the youngest age which migrates among populations.

Enter oldest age to migrate:

Enter the oldest age at which animals migrate.



```
          Output file? VORT.100
     +---------------------------------------------------------------------------+
     |    Do you want data files produced for graphing? Y                        |
     +---------------------------------------------------------------------------+
          How many times do you want the simulation repeated? 100
          How many years do you want the simulation to run? 100
          At what time interval do you want extinction reports? 5
          How many populations do you want to model? 3
     +---------------------------------------------------------------------------+
     |    Enter youngest age to migrate:1                                        |
     |    Enter oldest age to migrate:5                                          |
     |    Enter sex that migrates (F=females, M=males, B=both):B                 |
     |    Enter probability of survival during migration: 50.00                 |
     |    Enter migration rates for both sexes, age 1 through 5:                 |
     |         from population  1 to population  2: 0.01000                      |
     |         from population  1 to population  3: 0.01000                      |
     |         from population  2 to population  1: 0.01000                      |
     |         from population  2 to population  3: 0.01000                      |
     |         from population  3 to population  1: 0.01000                      |
     |         from population  3 to population  2: 0.01000                      |
     +---------------------------------------------------------------------------+
          What is the maximum number of young per litter? 2
          Is reproduction density dependent? N
   ****************************************************************************
          Enter an integer. Minimum of 1, maximum of 250.
```

Figure 1-4.

Enter sex that migrates (F=females, M=males, B=both):

Specify whether males, females, or both are the dispersing sex.

Enter the probability of survival during migration:

Enter the survival rate (as a percent) of individuals that are migrating between populations. Dispersal mortality is imposed in addition to other mortality.

Enter migration rates for [males/females/both sexes], age [x] through [y]:

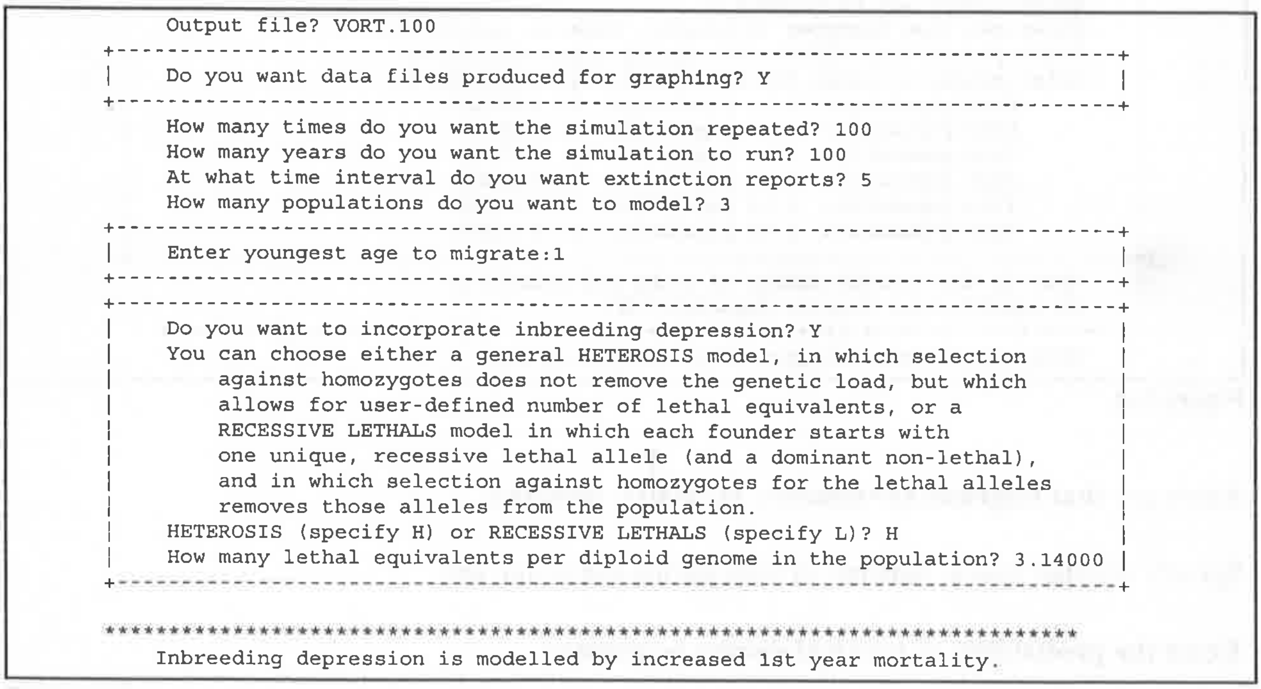
Enter these rates as probabilities for each animal within the specified age range and of the specified sex(es) within a given population to move to the stipulated population each year. That is, enter `0.01` for a 1% probability that an animal in population #1 will migrate to population #2 in any given year.

Migration rates need not be symmetric among populations; enter whatever probability you deem appropriate for each population. However, migration rates cannot be varied between years within a given population. The minimum probability accepted is `0.00001`. You may also enter `0.0` for no probability of transfer between two populations. VORTEX asks for migration rates for all the possible combinations for movement among populations. Probabilities greater than 10% (0.10) usually represent a functionally contiguous population as opposed to true metapopulations.

Do you want to incorporate inbreeding depression? (Figure 1-5)

The answer to this question may be crucial for your simulation. A brief discussion of this topic will follow. However, if you are not familiar with the concepts underlying inbreeding depression, you are advised to consult Chapters 2 through 5, and papers by Ralls et al. (1988) and Lacy (1992 and 1993a).

Inbreeding (mating between close relatives) may or may not affect the ability of an animal to survive or to reproduce. If you suspect, or have data to support, that inbreeding may produce deleterious effects in your species, enter `Y`.



```
        Output file? VORT.100
     +------------------------------------------------------------------------+
     |  Do you want data files produced for graphing? Y                       |
     +------------------------------------------------------------------------+
        How many times do you want the simulation repeated? 100
        How many years do you want the simulation to run? 100
        At what time interval do you want extinction reports? 5
        How many populations do you want to model? 3
     +------------------------------------------------------------------------+
     |  Enter youngest age to migrate:1                                       |
     +------------------------------------------------------------------------+
     +------------------------------------------------------------------------+
     |  Do you want to incorporate inbreeding depression? Y                   |
     |  You can choose either a general HETEROSIS model, in which selection   |
     |      against homozygotes does not remove the genetic load, but which   |
     |      allows for user-defined number of lethal equivalents, or a        |
     |      RECESSIVE LETHALS model in which each founder starts with         |
     |      one unique, recessive lethal allele (and a dominant non-lethal),  |
     |      and in which selection against homozygotes for the lethal alleles |
     |      removes those alleles from the population.                        |
     |  HETEROSIS (specify H) or RECESSIVE LETHALS (specify L)? H             |
     |  How many lethal equivalents per diploid genome in the population? 3.14000 |
     +------------------------------------------------------------------------+

     ***********************************************************************
       Inbreeding depression is modelled by increased 1st year mortality.
```

Figure 1-5.

At the beginning of the simulation, each animal is assigned two unique alleles. Each offspring created by these initial animals is randomly assigned one of the two alleles from each parent. Inbreeding depression is modeled as a reduction in survival during the FIRST YEAR among inbred animals. VORTEX usually underestimates the impact of inbreeding, as inbreeding often also depresses other components of fitness such as adult survival, success in competition for mates, and fecundity.

Although other impacts of inbreeding, such as reduced fecundity, are not modeled by VORTEX, you can mimic such a reduction by altering the percent survival in the first year. Thus, if fully inbred animals have fecundity reduced by 50%, this can be modeled by increasing the "lethal equivalents" (see below) in the simulation model by 0.50, thereby killing about half of offspring in addition to those killed by other factors (including the effect of inbreeding on first-year survival).

VORTEX offers two models of inbreeding depression: the Recessive Lethals model and the Heterosis model. In the Recessive Lethals model, each founder starts with one unique recessive, lethal allele and a unique, dominant, non-lethal allele. This model approximates the effect of inbreeding if each individual in the starting population had one recessive, lethal allele somewhere in its genome. When an offspring receives two matching, recessive, lethal alleles (i.e., is homozygous), it is removed from the population. As a result, lethal alleles are slowly removed from the population by natural selection. This reduces the population's genetic variation, but it also lessens the subsequent probability that inbred individuals would be homozygous for a lethal allele. This model gives an optimistic reflection of the impacts of inbreeding on many wildlife populations, in that most vertebrate populations contain more than one lethal allele per individual, on average (Ralls et al. 1988), and selection is unlikely to be wholly effective at removing the deleterious alleles from an inbreeding population (Brewer et al. 1990; Lacy 1992). The Recessive Lethals model runs *much* faster than the Heterosis model, however.

In the Heterosis model, you are allowed to enter the number of "lethal equivalents". A population with the level of inbreeding depression of one lethal equivalent per diploid genome may have one recessive lethal allele per individual (as in the Recessive Lethals model); or it may have two recessive alleles per individual, each of which confers a 50% decrease in survival; or it may have some combination of recessive deleterious alleles which equate with one fully lethal allele per individual. Natural selection does not remove deleterious alleles at heterotic (or over-dominant) loci, because all alleles in this model are partly deleterious when homozygous. Thus, under this model the effects of inbreeding are unchanged during repeated generations of inbreeding.

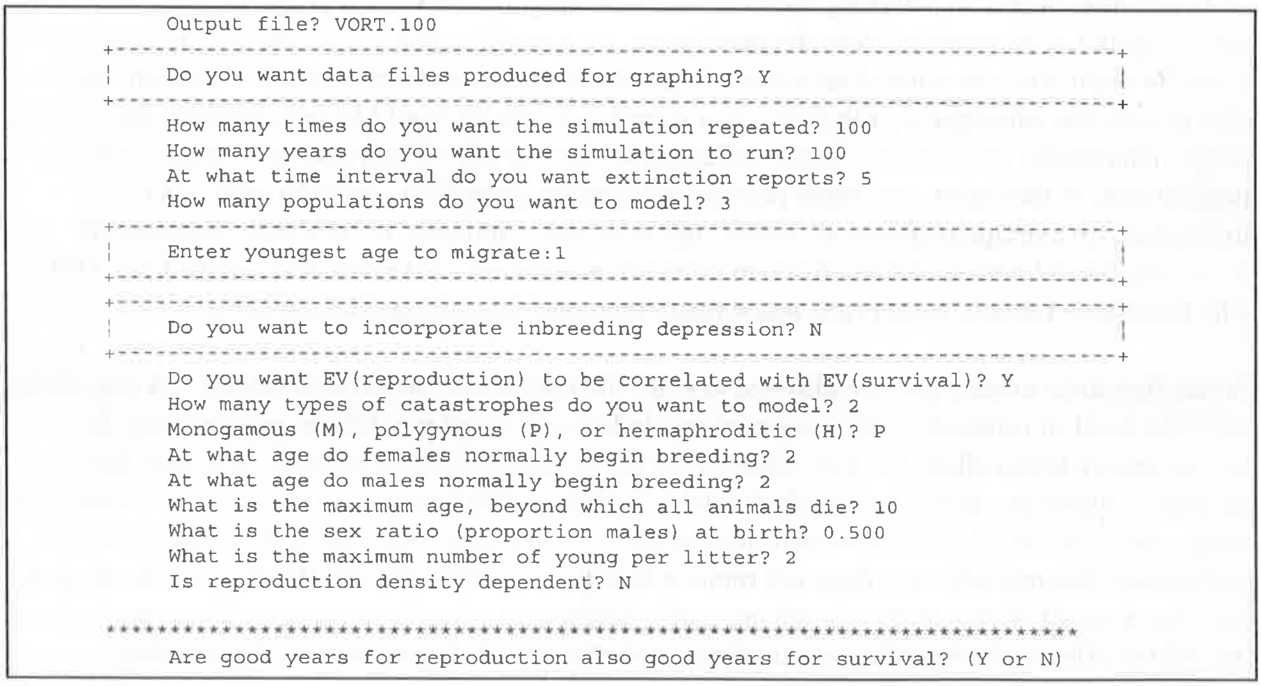
The default number of lethal equivalents for the Heterosis model is 3.14, which is the median value obtained in a study of 40 mammalian species (Ralls et al. 1988). Similar surveys of lethal equivalents currently do not exist for non-mammalian species.

Enter `H` for the Heterosis model or `L` for the recessive Lethals model; if `H` is entered, you can accept the default value of 3.140 lethal equivalents or enter your own value. It would be wise to be able to justify (to yourself, if no one else!) your selection of lethal equivalents should you enter your own value.

Do you want EV (reproduction) to be correlated with EV (survival)? (Figure 1-6)

Environmental variation (EV) is the annual variation in the probabilities of reproduction and survival that occur because of changes in the environment. EV impacts all individuals in the population simultaneously. The sources of EV are outside of the population; examples include weather, predator and prey populations, and parasite loads. These factors can affect reproduction and survival independently or simultaneously. For example, a reduction in food supply can reduce reproduction as well as survival. Enter **Y** for yes if you feel that good years for reproduction are also good years for survival.

Note: You define what stage of the life cycle is considered to be reproduction; VORTEX doesn't care. Reproduction in mammals is usually defined as birth. In birds, reproduction can be defined as an egg laid or as a chick fledged. For amphibians, reproduction can even be defined as metamorphosis.



```
       Output file? VORT.100
  +----------------------------------------------------------------------------+
  |    Do you want data files produced for graphing? Y                         |
  +----------------------------------------------------------------------------+
       How many times do you want the simulation repeated? 100
       How many years do you want the simulation to run? 100
       At what time interval do you want extinction reports? 5
       How many populations do you want to model? 3
  +----------------------------------------------------------------------------+
  |    Enter youngest age to migrate:1                                         |
  +----------------------------------------------------------------------------+
  +----------------------------------------------------------------------------+
  |    Do you want to incorporate inbreeding depression? N                     |
  +----------------------------------------------------------------------------+
       Do you want EV(reproduction) to be correlated with EV(survival)? Y
       How many types of catastrophes do you want to model? 2
       Monogamous (M), polygynous (P), or hermaphroditic (H)? P
       At what age do females normally begin breeding? 2
       At what age do males normally begin breeding? 2
       What is the maximum age, beyond which all animals die? 10
       What is the sex ratio (proportion males) at birth? 0.500
       What is the maximum number of young per litter? 2
       Is reproduction density dependent? N

  ****************************************************************************
       Are good years for reproduction also good years for survival? (Y or N)
```

Figure 1-6.

How many types of catastrophes do you want to model?

Catastrophes can be thought of as the extreme of environmental variation. Catastrophes are events that impact either reproduction or survival. Catastrophes can be habitat destruction, floods, fire, disease, etc. You determine what type(s) of catastrophe, if any, may impact your population. Despite what many think, catastrophes do happen and are very real considerations when attempting to model the fate of small populations. Later on in VORTEX, you will be given the opportunity to define what the impact of these catastrophes may have on reproduction and survival. You may be able to identify historical catastrophes by examining birth and death rates of your species of interest. A catastrophe may have occurred when a rate is noted that statistically higher than the normal variation.

Monogamous (M), polygynous (P), or hermaphroditic (H) breeding?

The breeding system modeled by VORTEX assumes that mates are randomly reshuffled each year and that all animals that can breed have an equal probability of breeding. Some animals may be excluded from breeding, however, and later in the program, you will be given an opportunity to define the breeding pool. If you enter `M` for monogamous mating, there must be a male for each female; thus males may become a limiting factor restricting breeding. If you enter `P` for polygynous, then there needs to be at least one male breeder for all breeding females. This may not reflect biological reality because, depending upon your input parameters and random births/deaths, your population may have one male breeding hundreds of females. VORTEX cannot fully customize polygynous mating because of the complexity of considering all the different species. More complex breeding systems can substantially impact genetic variation (usually negatively), but are less likely to seriously change the demographic performance of the population. If you enter `P` for polygynous breeding, you will later be asked to specify the degree of polygyny (e.g., the average number of mates per breeding male).

VORTEX also allows the modeling of a species with hermaphroditic breeding; that is, a species in which each individual is both sexes and can potentially mate with any other individual. If you specify hermaphroditic breeding (`H`), then you will later be asked to specify the frequency of selfing in the population. Selfing is assumed to consist of sexual reproduction (i.e., haploid gametes with a randomly assigned allele at each genetic locus combine to form the diploid offspring); not asexual, clonal reproduction. In the case of a hermaphroditic species, VORTEX labels all individuals as females.

At what age do females normally begin breeding?

VORTEX defines breeding as the time when the first young are born, not the age of sexual maturity or the age of first conception. For example, if an elephant breeds at age 10, but doesn't calve until age 12, then enter `12` as the age when female elephants normally begin breeding. VORTEX also assumes discrete intervals (usually years, but whatever you define as a time cycle). Thus, breeding age must be an integer. You cannot enter 2.5 years as the first age of breeding; it must be either `2` or `3`. You should enter the median age of first breeding, not the earliest age ever observed, as the earliest age of breeding may be atypical of the normal population behavior.

At what age do males normally begin breeding?

The same rule for females applies to males. Thus, if male elephants breed at age 10, and their offspring are born two years later, enter `12` as the first year of breeding for male elephants.

What is the maximum age, beyond which all animals die?

VORTEX assumes that animals can breed (at the species typical rates) throughout their adult lifespans. Do not enter the maximum life expectancy of your species if the species does not reproduce throughout its entire life. Thus, if individuals have been recorded as living as long as 10 years, but they cease reproduction at age 5, then enter `5` as the maximum age.

What is the sex ratio (proportion males) at birth?

Enter a number between 0.0 and 1.0 to represent the average proportion of births that are male. This is usually 50% (enter `0.5`), representing a 50:50 sex ratio at birth. If more or fewer males are born, enter the number accordingly (e.g., `0.55` for 55% male births).

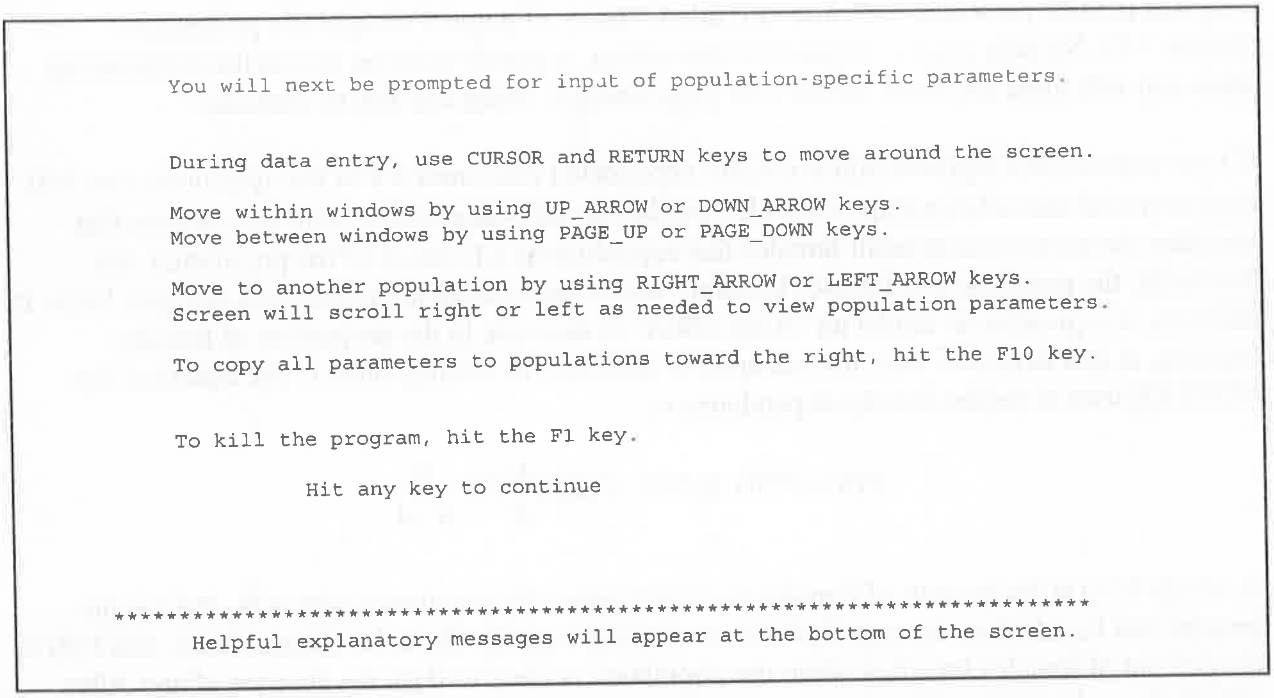
What is the maximum number of young per litter?

This question is answered by entering the most individuals born in a litter. You may wish to enter clutches or pods instead of litters depending on the appropriate terminology for your taxon. If your species produces more than one litter per year, but you are using years as the time cycle, then add and enter the total number of individuals born during the year. The number entered will be the maximum annual reproduction allowed by VORTEX. You can enter the maximum number that has ever been observed, even though such an event might be rare, and later on in the program give that maximum size a low probability of occurrence.

Is reproduction density dependent?

Does the reproductive rate of your species change with changing population size? That is, is reproduction low when the population is low due to difficulty in finding mates or, conversely, does reproduction drop off when the population is high due to limited resources, limited territories, intraspecific strife, crowding, stress, etc.? If you enter `Y`, you will be later asked to provide additional parameters defining density dependence.

You will next see a screen (Figure 1-7) providing information on subsequent data entry. The directions listed apply only to subsequent screens and not to data previously entered. Subsequent data relate to specific populations and you will be allowed to move within and among those populations to enter or edit data.



```
        You will next be prompted for input of population-specific parameters.


        During data entry, use CURSOR and RETURN keys to move around the screen.

        Move within windows by using UP_ARROW or DOWN_ARROW keys.
        Move between windows by using PAGE_UP or PAGE_DOWN keys.

        Move to another population by using RIGHT_ARROW or LEFT_ARROW keys.
        Screen will scroll right or left as needed to view population parameters.

        To copy all parameters to populations toward the right, hit the F10 key.


        To kill the program, hit the F1 key.

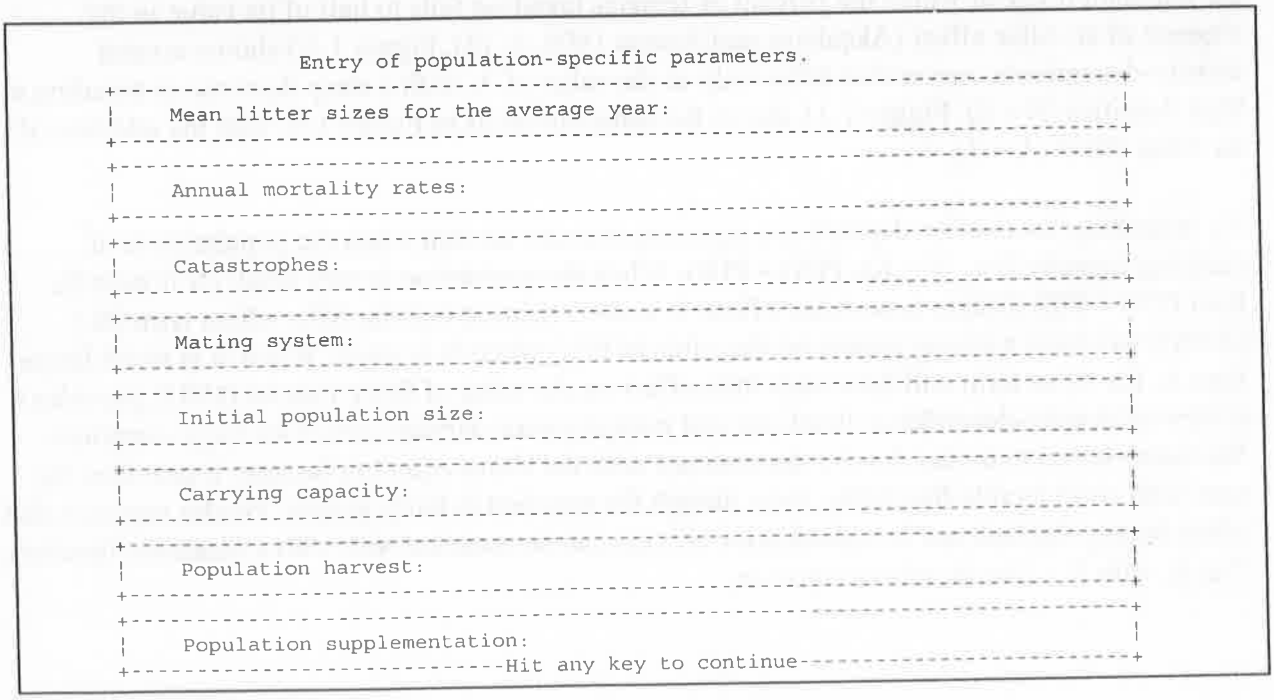
                  Hit any key to continue




    ****************************************************************************
         Helpful explanatory messages will appear at the bottom of the screen.
```

Figure 1-7.

As before, data can be entered using the Enter key or by moving the cursor. To move between windows, use Page Up or Page Down keys. To move within a window and within a population, use Up Arrow (↑) or Down Arrow (↓) keys. To move to another population within a window, use Left Arrow (←) or Right Arrow (→) keys. At this point, hit any key to continue.



```
               Entry of population-specific parameters.
    +-----------------------------------------------------------------+
    |   Mean litter sizes for the average year:                       |
    +-----------------------------------------------------------------+
    +-----------------------------------------------------------------+
    |    Annual mortality rates:                                      |
    +-----------------------------------------------------------------+
    +-----------------------------------------------------------------+
    |    Catastrophes:                                                |
    +-----------------------------------------------------------------+
    +-----------------------------------------------------------------+
    |    Mating system:                                               |
    +-----------------------------------------------------------------+
    +-----------------------------------------------------------------+
    |    Initial population size:                                     |
    +-----------------------------------------------------------------+
    +-----------------------------------------------------------------+
    |    Carrying capacity:                                           |
    +-----------------------------------------------------------------+
    +-----------------------------------------------------------------+
    |    Population harvest:                                          |
    +-----------------------------------------------------------------+
    +-----------------------------------------------------------------+
    |    Population supplementation:                                  |
    +---------------------------Hit any key to continue---------------+
```

Figure 1-8.

You will next be presented with a screen titled, “Entry of population-specific parameters” (Figure 1-8). No data entry is required at this screen; it merely informs you of the forthcoming areas that will more precisely define your population(s). Press any key to continue.

If your population's reproduction is density dependent (you entered `Y` to that question), you will need to model this relationship. VORTEX models density-dependence with an equation that specifies the proportion of adult females that reproduce as a function of the population size. Normally, the proportion of females breeding would decrease as the population size gets large. In addition, it is possible to model an “Allee effect” (a decrease in the proportion of females breeding at low densities, due, for example, to difficulty in finding mates). The equation that VORTEX uses to model density-dependence is:

$$P(N)=(P(0)-[(P(0)-P(K))(\frac{N}{K})^{B}])\frac{N}{N+A}$$

in which P(N) is the percent of females that breed when the population size is N, P(K) is the percent that breed when the population is at carrying capacity (K, to be entered later), and P(0) is the percent of females breeding when the population is close to 0 (in the absence of any Allee effect). B can be any positive number. The exponent B determines the shape of the curve relating percent breeding to population size, as population size gets large. If B is 1, the percent breeding changes linearly with population size. If B is 2, P(N) is a quadratic function of N. Figure 1-9 shows representative density-dependence curves for some values of B.

The term A in the density-dependence equation defines the Allee effect. One can think of A as the population size at which the percent of females breeding falls to half of its value in the absence of an Allee effect (Akçakaya and Ferson 1990, p. 18). Figure 1-10 shows several density-dependence curves that differ only in the value of A, with a steep decrease in breeding at high densities (B = 8). Figure 1-11 shows the same curves as in Figure 1-9, with the addition of an Allee effect (A = 1).

By inspecting the density-dependence equation, one can see that when the population is at carrying capacity (i.e., N = K), P(N) = P(K). When the population is very small (N is near 0), then P(N) = P(0) if there is no Allee effect. It is also apparent that the Allee effect term [N / (A+N)] will have a strong impact on the value of P(N) when N is small. When N is much larger than A, the Allee term will have very little effect on the value of P(N). Fowler (1981) provides a review of density-dependence functions and presents some density-curves for large mammals. We have chosen to model density-dependence with the above equation because it provides the user with considerable flexibility, even though the equation is fairly simple. Fowler suggests that often density-dependence in reproductive success can be modeled well with a quadratic function, that is, with B = 2 in the above equation.

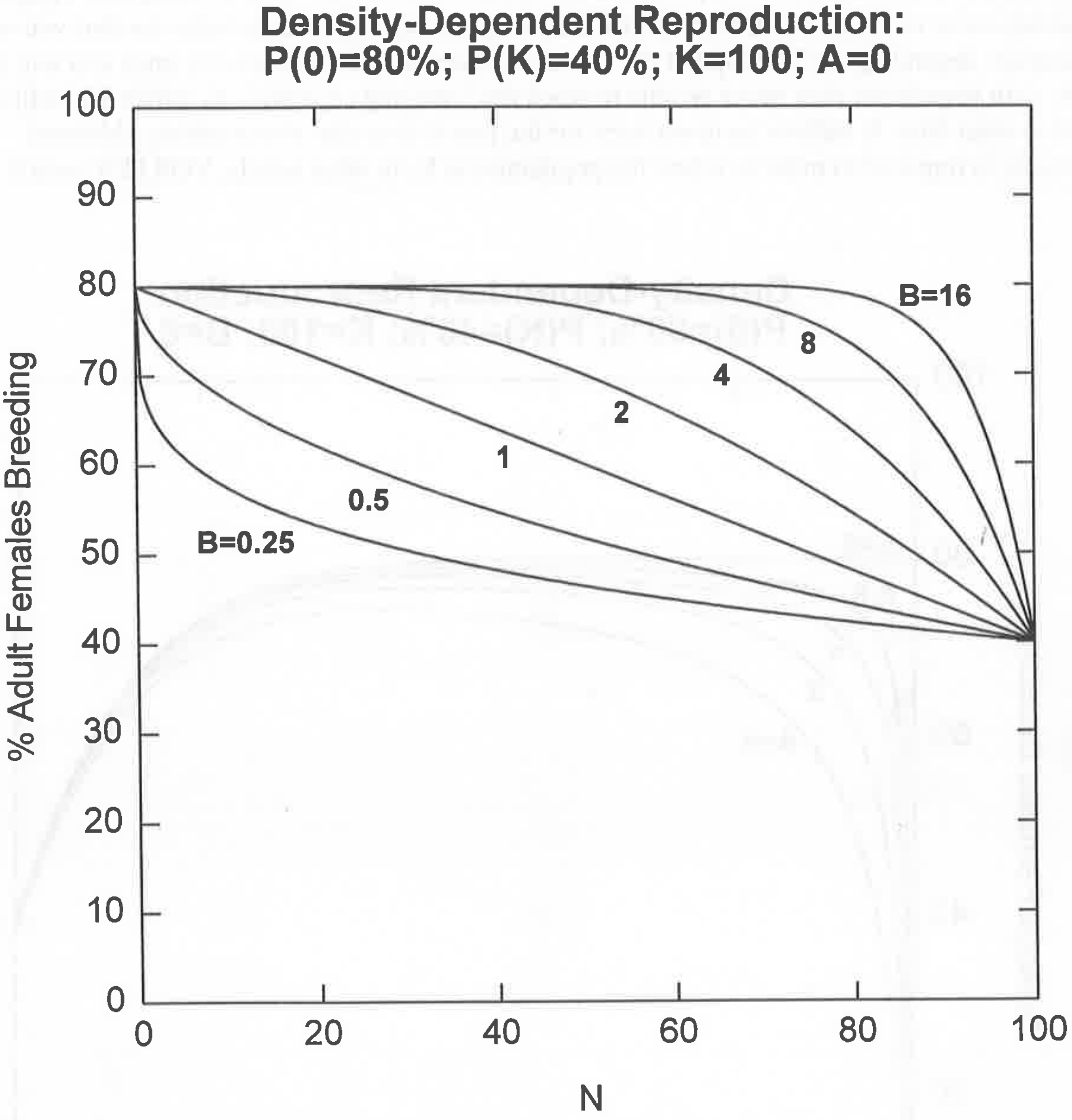


Figure 1-9.

It is best to derive the values of A, B, P(0), and P(K) from a regression analysis of data on the breeding rate of your population. If these data are unavailable, but you can estimate P(0) and P(K), then you may want to explore several different combinations of the A and B parameters to arrive at a curve that seems appropriate for your population. You could use graphics or statistical software (or even graph paper and a calculator) to construct a range of hypothetical curves, using different combinations of parameters, as was done to produce Figures 1-9 through 1-11. In any case, once you have decided on a particular set of parameters to use, you should always graph the resulting curve to verify that it represents the kind of density-dependence behavior that you want. A caution: depending on the shape of the curve you specify, and the mortality rates you will enter later, your population may never be able to reach the "carrying capacity", K, which you will also need to enter later. K defines an upper limit for the population size, above which additional mortality is imposed in order to return the population to K. In other words, VORTEX uses K to

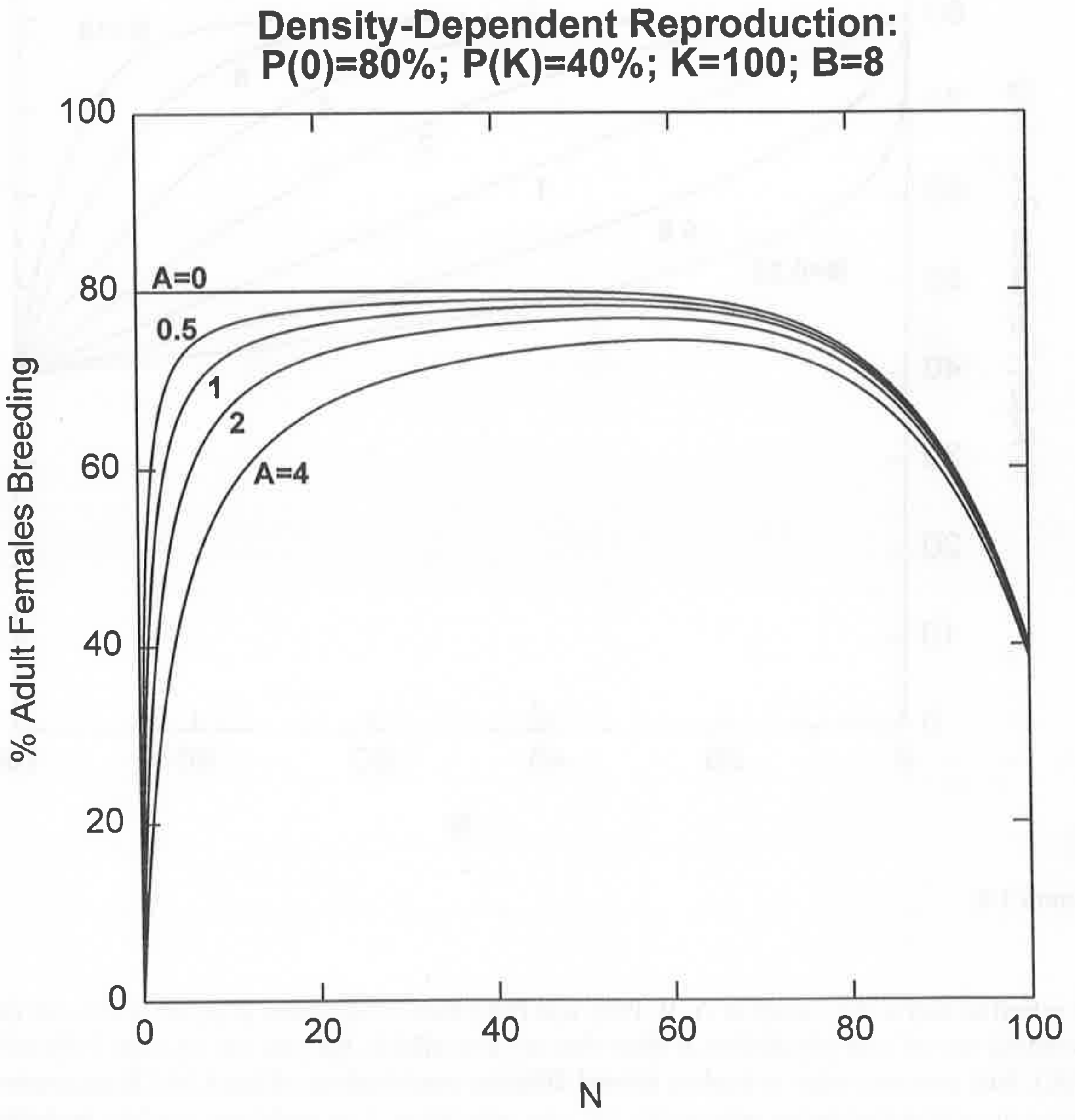


Figure 1-10.

impose a ceiling model of density-dependence on survival rates. The combination of density-dependence in reproduction and density-dependence in survival will determine over what range of population sizes the population is expected to experience average net growth, and over what range the population would be expected to decline because deaths outnumber births.

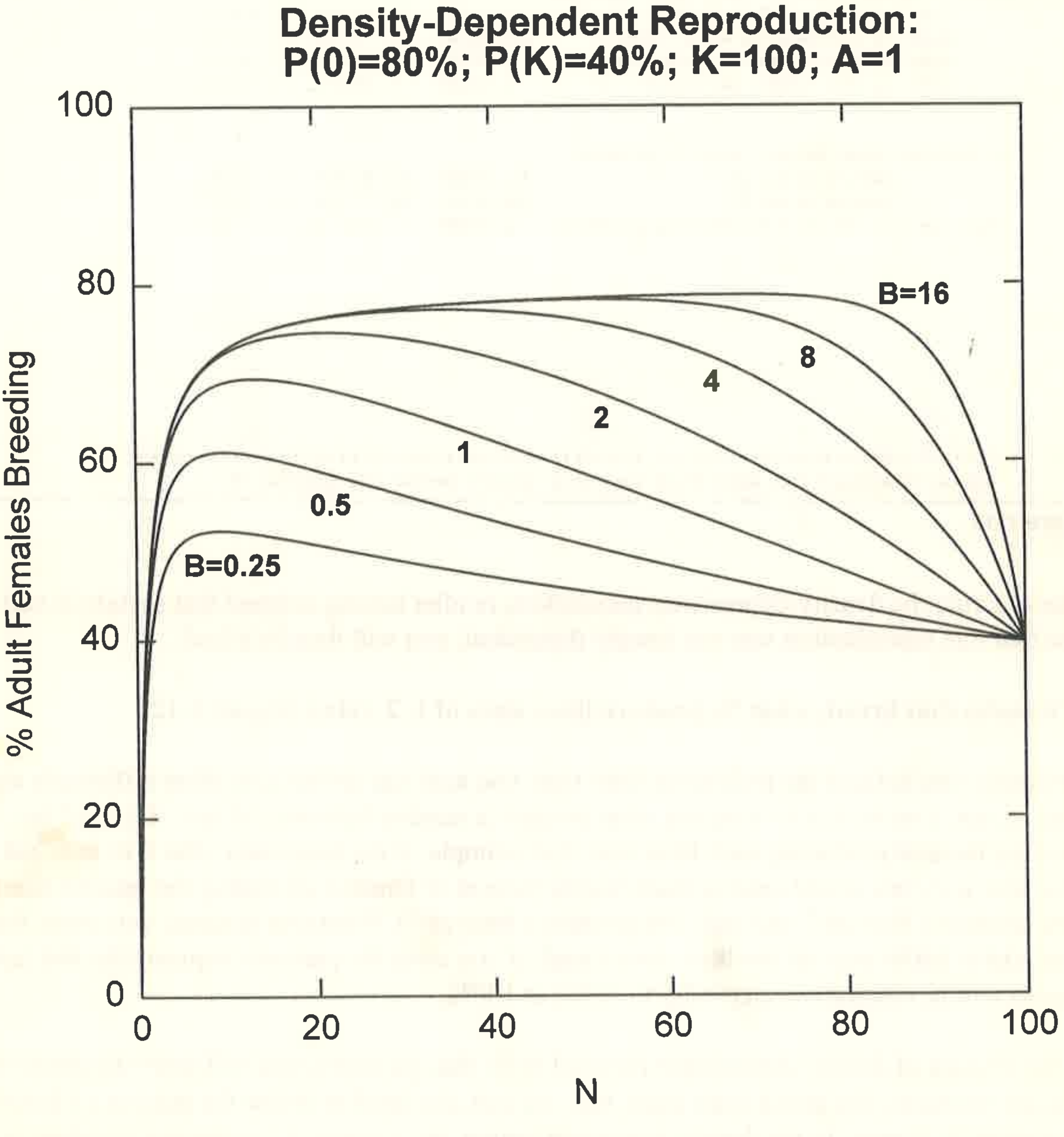
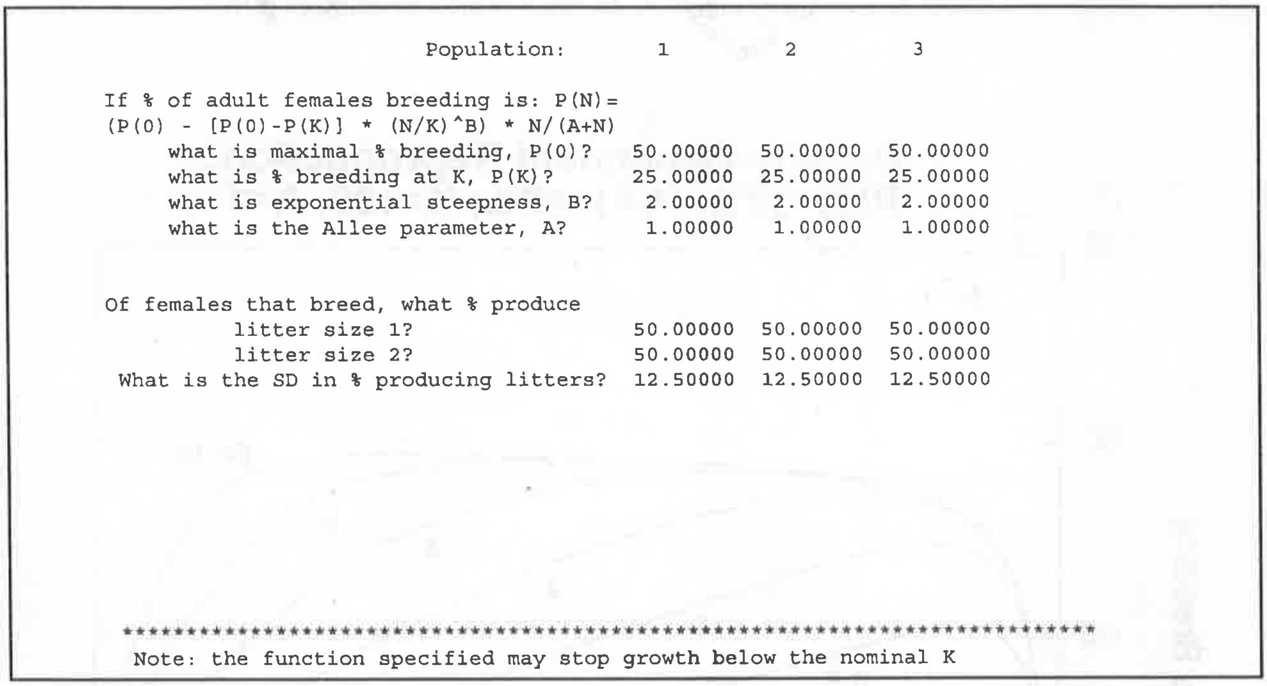


Figure 1-11.

Figure 1-12 illustrates the input screen for the density-dependence parameters. You are asked to enter P(0), P(K), B, and A, in that order, for each population. The parameters need not be the same for all populations.



```
                         Population:        1         2         3

If % of adult females breeding is: P(N)=
(P(0) - [P(0)-P(K)] * (N/K)^B) * N/(A+N)
     what is maximal % breeding, P(0)?   50.00000  50.00000  50.00000
     what is % breeding at K, P(K)?      25.00000  25.00000  25.00000
     what is exponential steepness, B?     2.00000   2.00000   2.00000
     what is the Allee parameter, A?       1.00000   1.00000   1.00000


Of females that breed, what % produce
          litter size 1?                 50.00000  50.00000  50.00000
          litter size 2?                 50.00000  50.00000  50.00000
 What is the SD in % producing litters?  12.50000  12.50000  12.50000





 ****************************************************************************
  Note: the function specified may stop growth below the nominal K
```

Figure 1-12.

After entering the density-dependence parameters, or after having skipped that section if you specified that reproduction was not density dependent, you will then be asked:

Of females that breed, what % produce litter sizes of 1, 2, (etc.) (Figure 1-12)

Previously you defined the maximum litter size; you now can define how often differently sized litters occur. You do this by entering what percent (a number between 0.0 and 100.0) of the breeding females producing each litter size. For example, if the maximum litter size is 5, but the usual size is 2, you would enter a much higher percent of females producing the smaller size (say 60% produce a litter of 2 and only 5% produce a litter of 5). Whatever percents you enter, they must add to 100% over all the litter sizes listed. If you enter the percents sequentially, the last percent will be entered automatically to arrive at 100%.

In the absence of density dependence (entered **N** for that question), you will enter the percents of females producing the stated litter sizes, but you will also need to define the percent of females producing NO litters. In the density dependent option, the percent of females not breeding is defined by the function describing the density-dependence.

In the case of hermaphroditic breeding, the percents of "females" producing each litter size refer to frequency of breeding *as a female*. Each mating takes place between a hermaphrodite acting in the female role and one in the male role (and they may be the same individual). If you specify that 75% of females produce litters (of various sizes), then VORTEX will have 75% of the hermaphrodites produce litters while functioning as females. Many of these individuals will also be used in the male role for breeding, as will some of the hermaphrodites not breeding as "females". Thus, more than 75% (about 94% in the case of no selfing) of the hermaphrodites will breed either in the role of females or in the male role.

At the end of the litter sizes, you will be asked:

What is the SD in % producing litters?

Environmental variation (EV) in reproduction is modeled by the user entering a standard deviation (SD) for the percent females producing litters. (This is the same as the SD in the percent not producing litters.) VORTEX then determines the percent breeding each year by sampling from a binomial distribution with the specified mean (e.g., 40%) and SD (e.g., 10%). About 66% of the time, the percent of females breeding will fall within ± 1 SD of the mean; about 95% of the time it will fall within ± 2 SD of the mean. Relative proportions of litters of each size (1, 2, etc.) are kept constant; what is varied from year to year is the percent breeding (litter size > 0) and the percent not breeding (litter size = 0). Note that if the percent producing litters is 100%, then the EV in reproduction will have no effect. This is the binomial distribution used for EV can have no variance if the mean is 100% or 0%.

Although the magnitude of environmental variation in birth and death rates can have a substantial impact on the viability of a population, it is often difficult to obtain the data needed to estimate EV. Long-term field studies are needed in order to determine the amount of fluctuation that occurs in demographic rates. If such data are available, the EV parameters can be calculated in the following manner:

The objective is to quantify the extent to which the reproductive rates (% of females producing offspring) and the mortality rates (see below) vary across years. One can get a first rough estimate of the required SDs (often about as accurate as one will get by more complex methods) in the following way:

- Calculate the % of females breeding, and age-sex specific mortalities, for each year for which there are data.

- The means across years give the overall mean % producing litters and the average annual mortalities.

- The variation (expressed as SDs) among the estimates across years gives the estimate of the fluctuations in the life table parameters due to environmental variation.

A common problem in estimating annual fluctuations in life table parameters is that the data might be so sparse that it is difficult or impossible to estimate the parameters on an annual basis. If this is the case, you might be forced to admit that the data are not sufficient to allow estimation of the SDs. The only alternatives are to guess at the fluctuations in reproductive and mortality rates, based on a general understanding of the natural history of the animal, or to omit environmental fluctuations altogether from the model (by entering `0` for each SD), recognizing that one component of instability is being ignored in the analyses.

Another problem with the above approach, which may add a significant bias if sample sizes are small, is that some of the year-to-year variation observed in reproductive and mortality rates would be due to the expected demographic stochasticity (luck of the draw) even if environmental variation causes no fluctuation in the probabilities of birth and death. To remove the expected demographic variation from the observed annual fluctuations (in order to leave just the environmental variation):

- Calculate the proportion breeding (or the age-sex specific mortality) for each year, and a mean across years.

- Calculate the observed variances across years in birth and death rates.

- For each year, estimate the expected variances in the rates as the binomial variance, p(1-p)/(N-1), in which p is the proportion breeding (or dying) and N is the sample size (number of adult females or number of animals at risk of dying) for that year. N-1 is needed instead of the usual N for a binomial variance to correct for bias that arises from using p estimated from the sample rather than the true (unknown) p.

- Subtract the mean expected variance (from step 3) from the observed inter-year variance (step 2), to yield the variance in excess of that expected by chance (i.e., the environmental variation) for each life table rate.

- Take square roots to convert environmental variances to SDs, and then multiply by 100 convert to percents (which is the way VORTEX asks for the data).

Thus, in order of ease of use (easiest to most difficult) and precision (least precise to most precise), options for estimating EV are: guess at the "typical" fluctuations in reproduction and mortality rates; calculate the variation across years in the rates, from long-term field data; adjust the observed variation by subtracting the variance due to demographic stochasticity (random sampling) even if *probabilities* of breeding or dying remain constant.

Enter mortalities of females as percents (Figure 1-13)

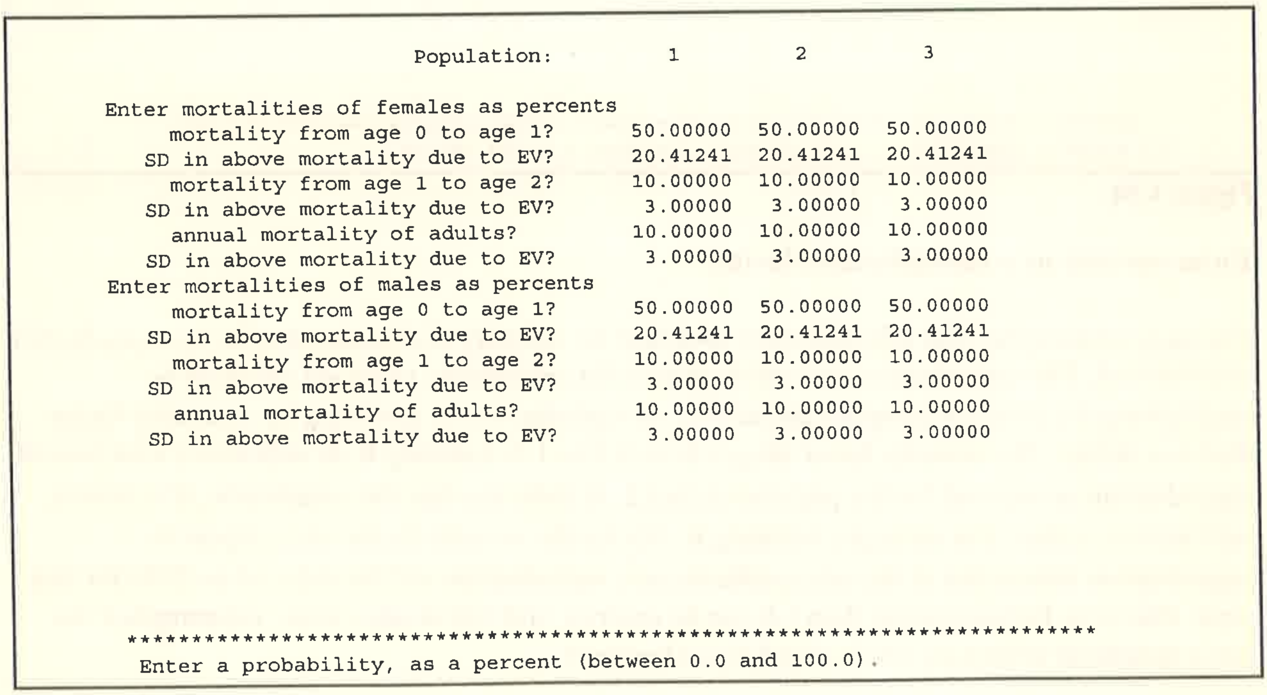
Here is where you define age class mortalities. Enter mortality as a percent (between 0.0 and 100.0) for each class or immature females. Once reproductive age is reached, the annual probability of mortality remains constant over the life of the animal and is entered only once.

SD in mortality due to EV?

You must enter a standard deviation (SD) due to environmental variation (EV) for each age class mortality. See the above discussion about methods of estimating these SDs. Be aware that if you enter an SD that is at least half of the survival rate (100% - mortality rate), then in occasional years the mortality rate will be set at 100% and the population will automatically go extinct. For example, if all age-specific mortality rates are 50%, and if the SDs representing EV are set at 25%, then about 1 in 40 years the mortality rate after adjustment for EV will be 100% (because we expect the rate to exceed the mean by 2 SDs about 2.5% of the time).

Enter mortalities of males as percents.

The same comments for female mortalities apply to males.



```
                      Population:          1          2          3

   Enter mortalities of females as percents
        mortality from age 0 to age 1?   50.00000   50.00000   50.00000
      SD in above mortality due to EV?   20.41241   20.41241   20.41241
        mortality from age 1 to age 2?   10.00000   10.00000   10.00000
      SD in above mortality due to EV?    3.00000    3.00000    3.00000
        annual mortality of adults?      10.00000   10.00000   10.00000
      SD in above mortality due to EV?    3.00000    3.00000    3.00000
   Enter mortalities of males as percents
        mortality from age 0 to age 1?   50.00000   50.00000   50.00000
      SD in above mortality due to EV?   20.41241   20.41241   20.41241
        mortality from age 1 to age 2?   10.00000   10.00000   10.00000
      SD in above mortality due to EV?    3.00000    3.00000    3.00000
        annual mortality of adults?      10.00000   10.00000   10.00000
      SD in above mortality due to EV?    3.00000    3.00000    3.00000

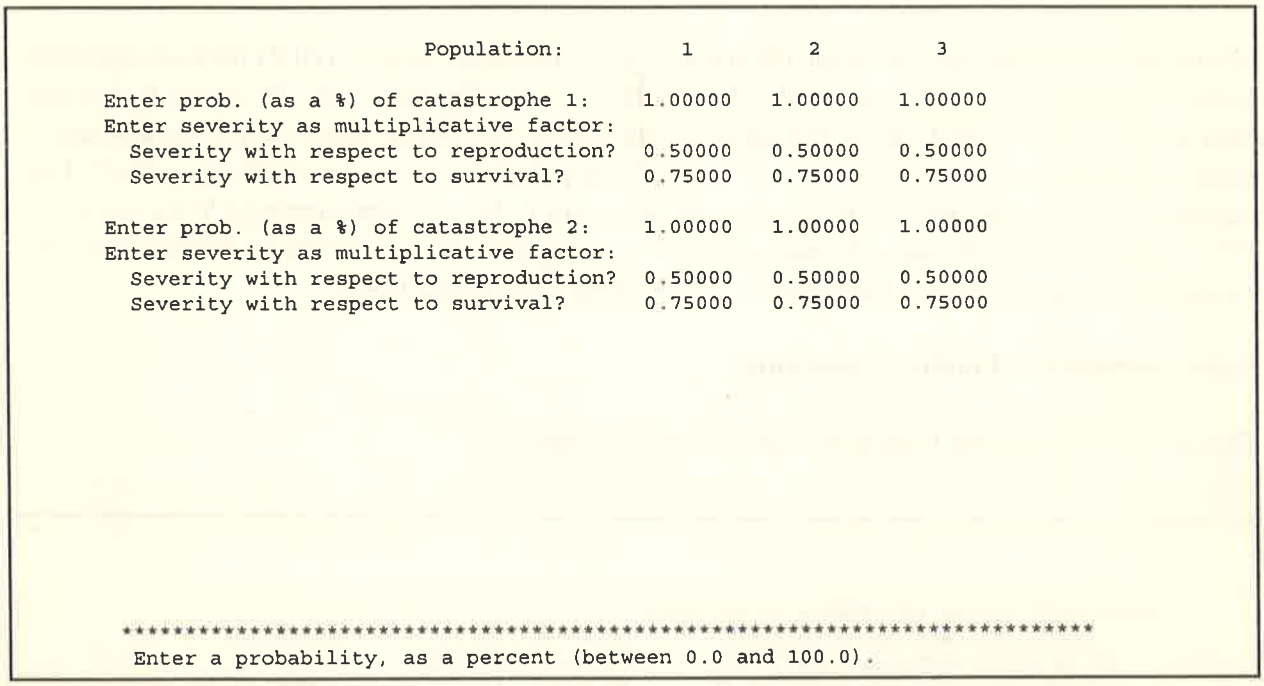



 ******************************************************************************
  Enter a probability, as a percent (between 0.0 and 100.0).
```

Figure 1-13.

Enter probability (as a %) of catastrophe 1: (Figure 1-14)

If you previously specified that one or more catastrophes will affect your population(s), you need now to define the probability of that catastrophe occurring each year. Enter this as a percent from 0.0 to 100.0. For example, value of `1.0` means that there is a 1 in 100 (1%) chance of the catastrophe occurring in any one year.



```
                              Population:          1          2          3

       Enter prob. (as a %) of catastrophe 1:    1.00000    1.00000    1.00000
       Enter severity as multiplicative factor:
         Severity with respect to reproduction?  0.50000    0.50000    0.50000
         Severity with respect to survival?      0.75000    0.75000    0.75000

       Enter prob. (as a %) of catastrophe 2:    1.00000    1.00000    1.00000
       Enter severity as multiplicative factor:
         Severity with respect to reproduction?  0.50000    0.50000    0.50000
         Severity with respect to survival?      0.75000    0.75000    0.75000









        ****************************************************************************
         Enter a probability, as a percent (between 0.0 and 100.0).
```

Figure 1-14.

Enter severity as a multiplicative factor:

For each catastrophe, you will also need to define the severity of this catastrophe on reproduction and survival. The reproduction and survival rates for catastrophe years are obtained by multiplying the (non-catastrophe) probability of reproduction or surviving by a severity factor that you define. The severity factor ranges from 0.0 to 1.0. Entering `0.0` indicates a total loss of reproduction or survival for the population and `1.0` indicates that the catastrophe, if it occurs, will have no effect. For example, entering `0.75` for the severity factor with respect to reproduction means that if the catastrophe occurs, reproduction will be reduced by 25% for that year. (Severity factors greater than 1.0 can be entered, and this would cause "catastrophes" to have beneficial effects on survival and reproduction.)

Enter probability (as a %) of catastrophe 2:

Enter data as for catastrophe 1 above if you chose more than one catastrophe.

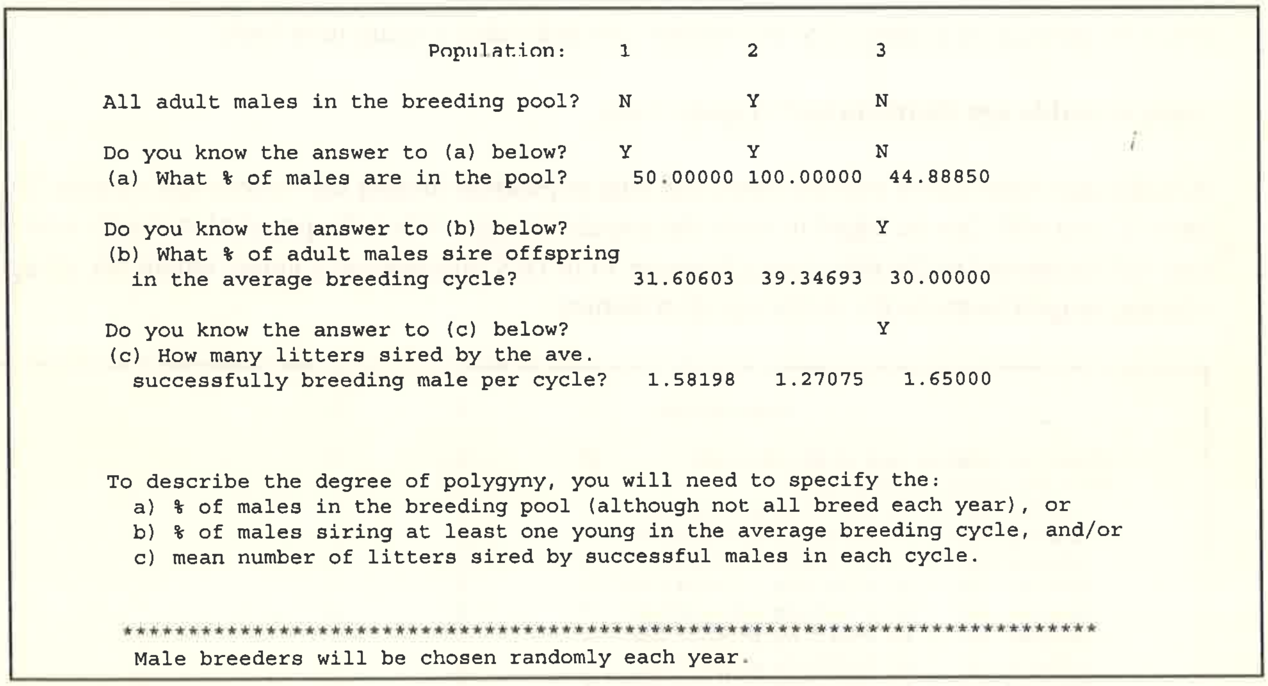
If you previously indicated that your species had a monogamous mating system (entered **M**), you will be asked the following two questions:

All adult males in the breeding pool? (Figure 1-15)

If you enter **Y**, you will be moved to the next screen (stable age distribution). If you enter **N**, answer the next question:

What % of adult males are in the pool?

Input the percent of breeding males for each population.



```
                              Population:    1         2         3

     All adult males in the breeding pool?   N         Y         N

     Do you know the answer to (a) below?    Y         Y         N
     (a) What % of males are in the pool?     50.00000 100.00000  44.88850

     Do you know the answer to (b) below?                        Y
     (b) What % of adult males sire offspring
       in the average breeding cycle?         31.60603  39.34693  30.00000

     Do you know the answer to (c) below?                        Y
     (c) How many litters sired by the ave.
       successfully breeding male per cycle?   1.58198   1.27075   1.65000



     To describe the degree of polygyny, you will need to specify the:
       a) % of males in the breeding pool (although not all breed each year), or
       b) % of males siring at least one young in the average breeding cycle, and/or
       c) mean number of litters sired by successful males in each cycle.

      ***************************************************************************
       Male breeders will be chosen randomly each year.
```

Figure 1-15.

If you previously indicated that your species had a polygynous mating system (entered **P**), you will be asked the following:

Are all adult males in the breeding pool?

If you enter **Y**, you will be moved to the next screen (stable age distribution). If you enter **N**, you will be presented with questions relating to those males capable of breeding. To describe the degree of polygyny, you will need to specify:

a) the percent of males in the breeding pool (although not all breed each year) OR
b) the percent of males siring at least one young in the average breeding cycle AND/OR
c) the mean number of litters sired by successful males in each cycle

If you know the answer to (a), enter `Y` and indicate what percent of males are in the breeding pool and DO NOT answer (b) or (c). Otherwise, answer (b) and/or (c); VORTEX will then calculate (a), based on the assumption that breeding success by males that are in the breeding pool is distributed according to a Poisson distribution.

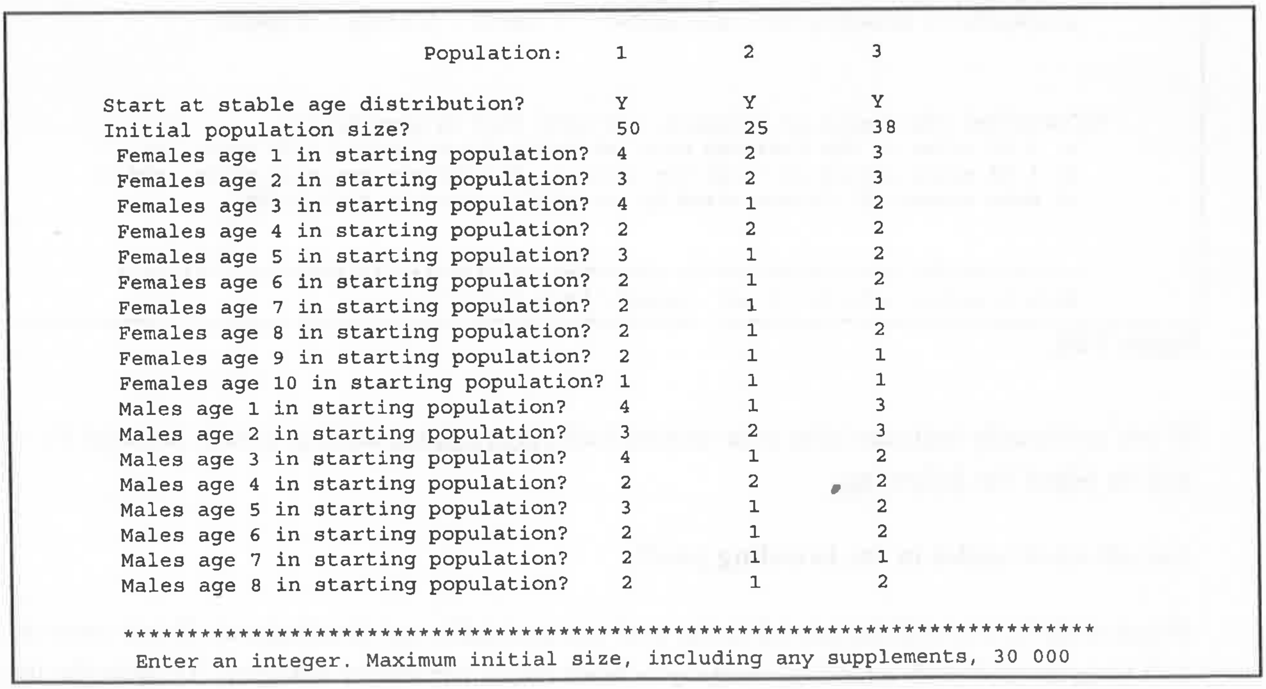
If you previously indicated that your species is <u>hermaphroditic</u>, you will be asked:

What % of breeding is selfing?

Enter the percent of matings that are selfing—an individual mating with itself.

Start at stable age distribution? (Figure 1-16)

A stable age distribution will distribute the total population among the various age classes. If you enter `Y`, you will then be asked to enter the population size. When the population size is entered, you will be moved to the next screen because VORTEX automatically enters values for all age classes, proportionate to the stable age distribution.



```
                         Population:     1          2          3

Start at stable age distribution?        Y          Y          Y
Initial population size?                 50         25         38
 Females age 1 in starting population?   4          2          3
 Females age 2 in starting population?   3          2          3
 Females age 3 in starting population?   4          1          2
 Females age 4 in starting population?   2          2          2
 Females age 5 in starting population?   3          1          2
 Females age 6 in starting population?   2          1          2
 Females age 7 in starting population?   2          1          1
 Females age 8 in starting population?   2          1          2
 Females age 9 in starting population?   2          1          1
 Females age 10 in starting population?  1          1          1
 Males age 1 in starting population?     4          1          3
 Males age 2 in starting population?     3          2          3
 Males age 3 in starting population?     4          1          2
 Males age 4 in starting population?     2          2          2
 Males age 5 in starting population?     3          1          2
 Males age 6 in starting population?     2          1          2
 Males age 7 in starting population?     2          1          1
 Males age 8 in starting population?     2          1          2

 ***************************************************************************
  Enter an integer. Maximum initial size, including any supplements, 30 000
```

Figure 1-16.

If you enter **N** for the first question, you will not be allowed to enter the total population size. Rather, the cursor will move to the first age class where you can enter the size of each age class for females and males.

Carrying capacity? (Figure 1-17)

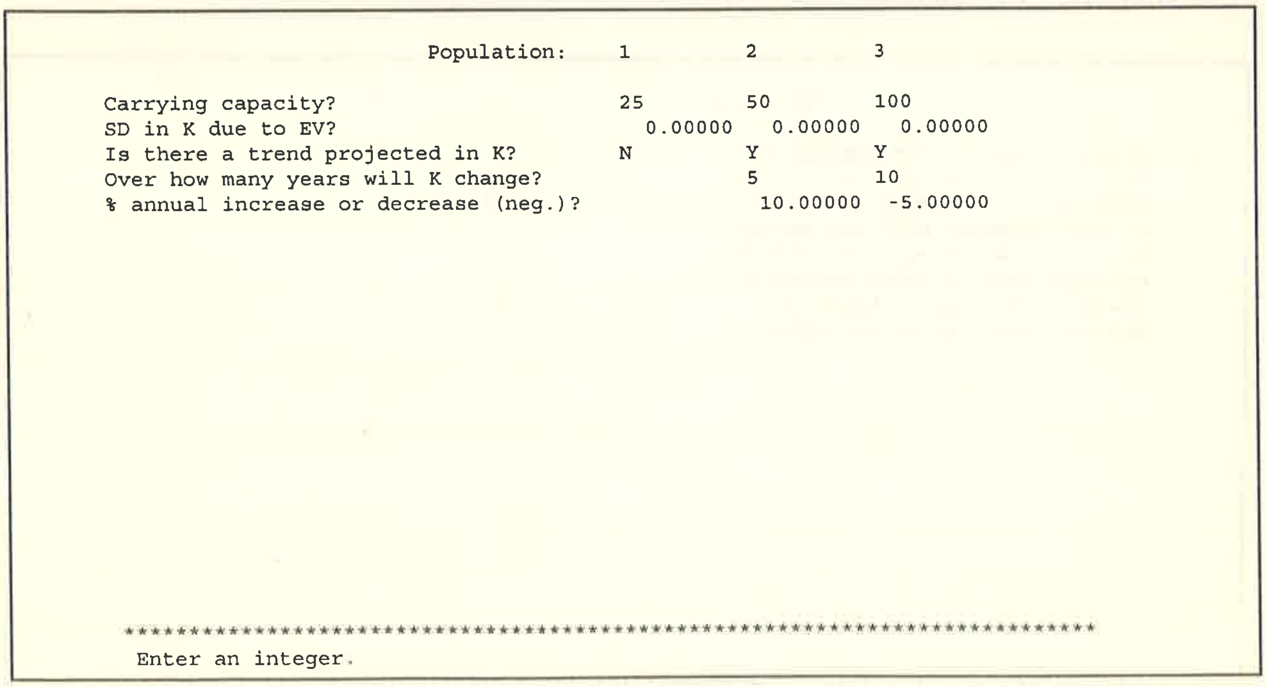
If the population increases above the carrying capacity value that you have entered, VORTEX will impose additional mortality on the population to bring it back down to that number. A mortality factor will be applied to all age classes and both sexes.

SD in K due to EV?

If carrying capacity (K) varies due to environmental variation (EV), enter a standard deviation (SD) to account for this variability. For example, the habitat might support different population sizes in different years due to changing conditions such as rainfall or food. The SD should be entered as a number of animals, not as a percent. That is if K = 2,000 with a SD of 10%, enter `200` (0.10 x 2000).

Is there a trend projected in K?

If you know or suspect that carrying capacity (K) will change, enter **Y** for yes. You will then be asked the following:



```
                          Population:     1          2          3

       Carrying capacity?                 25         50         100
       SD in K due to EV?                   0.00000    0.00000    0.00000
       Is there a trend projected in K?   N          Y          Y
       Over how many years will K change?            5          10
       % annual increase or decrease (neg.)?          10.00000   -5.00000










        **************************************************************************
        Enter an integer.
```

Figure 1-17.

Over how many years will K change?

Enter the number of years for which you expect carrying capacity (K) to change. VORTEX will model a linear change in K over these years.

% annual increase or decrease (neg.)?

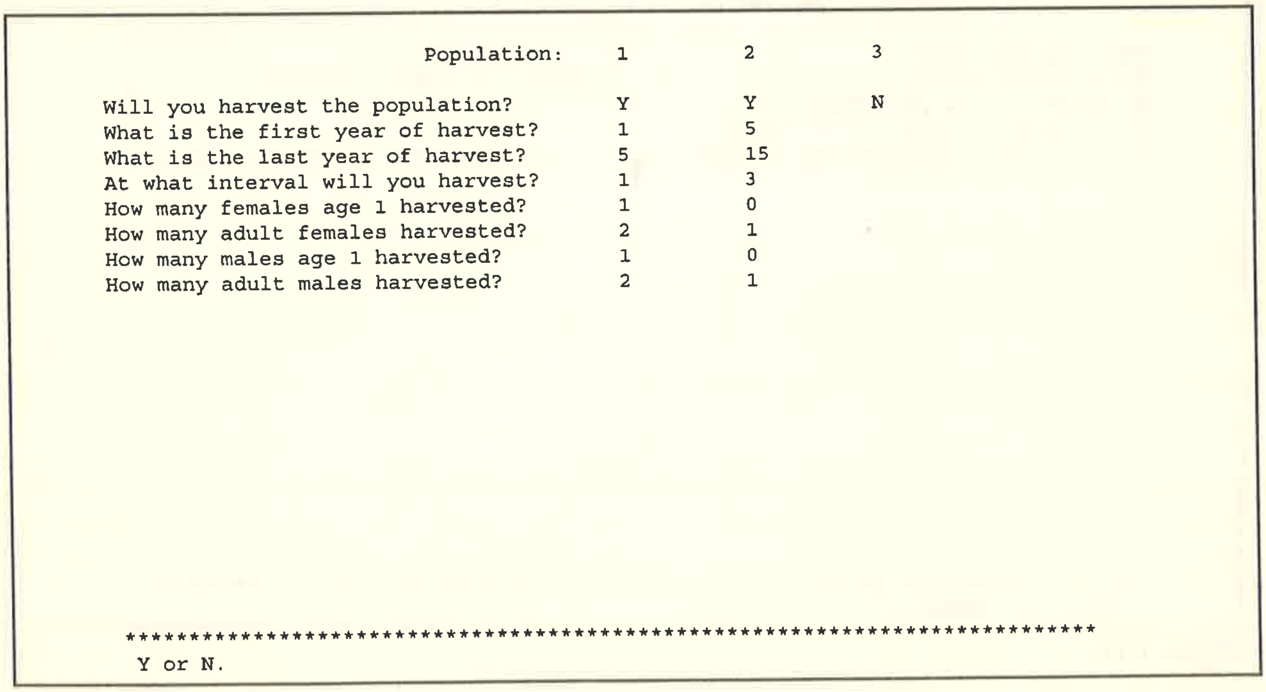
Enter the linear change in K as a percent between 0.0 and 100.0. If carrying capacity is expected to decrease, precede the percent with a negative (-) sign. A positive increase does not require a + sign.

Will you harvest the population? (Figure 1-18)

VORTEX gives you the option of removing animals. Harvesting can mimic hunting, culling, research, or even cyclic phenomena that result in deaths. It can reflect removal of young for translocation programs. If you entered `Y`, you will see the following questions; otherwise you will skip these questions.

What is the first year of harvest?

The harvest can begin (and end) at any time during the stipulated length of the simulation. Harvesting can also be cyclic (see later). Enter the year in which you wish to begin harvesting. For example, if you wish to harvest some animals in the 10th year of the simulation, enter `10`.



```
                               Population:    1         2         3

       Will you harvest the population?       Y         Y         N
       What is the first year of harvest?     1         5
       What is the last year of harvest?      5         15
       At what interval will you harvest?     1         3
       How many females age 1 harvested?      1         0
       How many adult females harvested?      2         1
       How many males age 1 harvested?        1         0
       How many adult males harvested?        2         1









         ****************************************************************************
          Y or N.
```

Figure 1-18.

What is the last year of the harvest?

Enter the last year that you wish to harvest animals. Remember, the first year and last year define the block of time in which harvesting can occur. You can further define periods within this time frame to harvest, but no harvest will be allowed before or after the time frame that you have defined.

At what interval will you harvest?

If you wish to harvest animals every year within the time frame that you have defined, enter `1`. If you wish to harvest animals every other year, enter `2`, etc. For example, if the first year of harvest is year 10, the last year is year 50, and the interval is 10 years, you will harvest animals at years 10, 20, 30, 40, and 50.

How many females of age 1, 2, etc. will you harvest?

Enter the number of juvenile females that you will harvest at each interval defined for each age class up to adults. Enter `0` for no females to be taken in a given age class. VORTEX harvests the animal the instant prior to calculating breeding, so the youngest animal that can be harvested is one year old. If VORTEX tries to harvest animals of an age class and finds that the animals do not exist, the simulation will continue (without the harvest of non-existent animals), but VORTEX will report at the end of the simulation that some of the attempted harvests could not be completed.

How many adult females harvested?

For harvesting, all females of breeding age are considered as "adults" and harvesting by chronological age is not an option. Each adult female, regardless of age, is equally likely to be harvested.

How many males of age 1, 2, etc. will you harvest?

Harvest juvenile males as you did juvenile females.

How many adult males harvested?

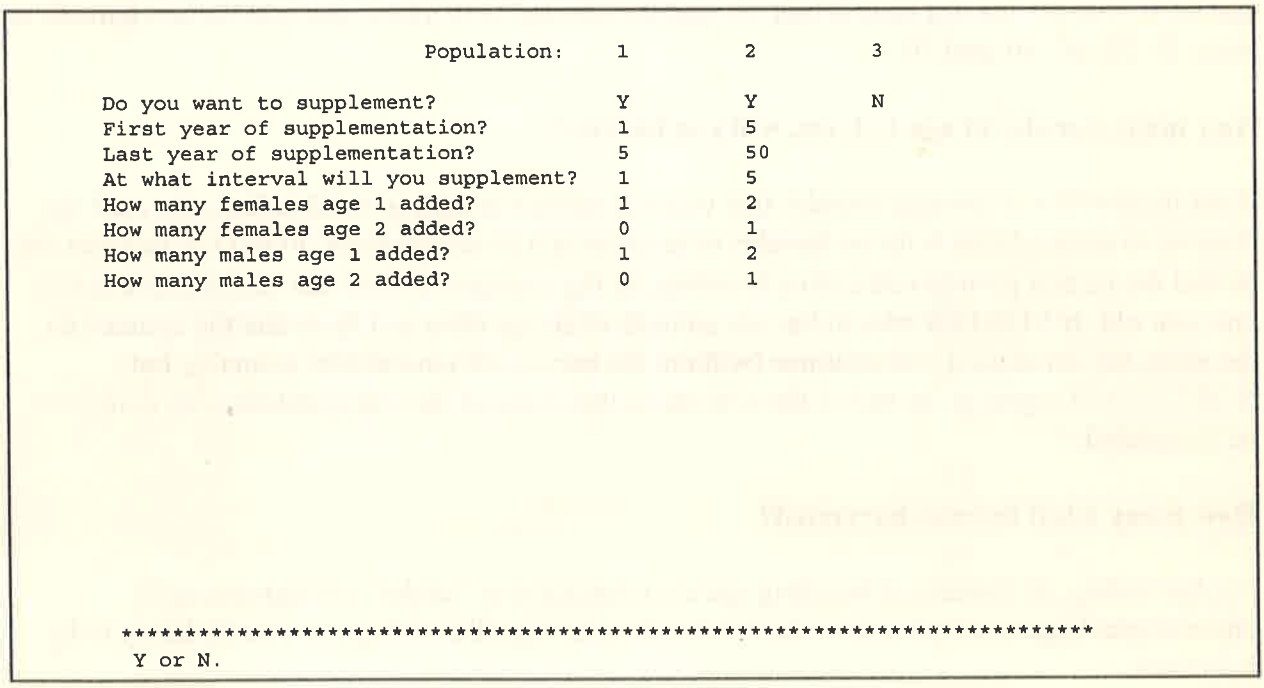
Harvest adult males as you did adult females.

Do you want to supplement? (Figure 1-19)

You have the option of adding any number of juvenile or adult, male or female animals to each population. They can be added at any time and interval within the time frame specified for the simulation. You may both harvest and supplement independent of each other. VORTEX assumes that the supplemented animals are not related to any animal in the receiving population. Thus, supplementation is a means of increasing genetic diversity, as well as animal numbers, within a population.

What is the first year of supplementation?
What is the last year of supplementation?
At what interval will you supplement?

Answer the above questions as you did for harvesting.



```
                             Population:     1         2         3

    Do you want to supplement?               Y         Y         N
    First year of supplementation?           1         5
    Last year of supplementation?            5         50
    At what interval will you supplement?    1         5
    How many females age 1 added?            1         2
    How many females age 2 added?            0         1
    How many males age 1 added?              1         2
    How many males age 2 added?              0         1











     ****************************************************************************
      Y or N.
```

Figure 1-19.

How many females age 1, 2, etc. added?

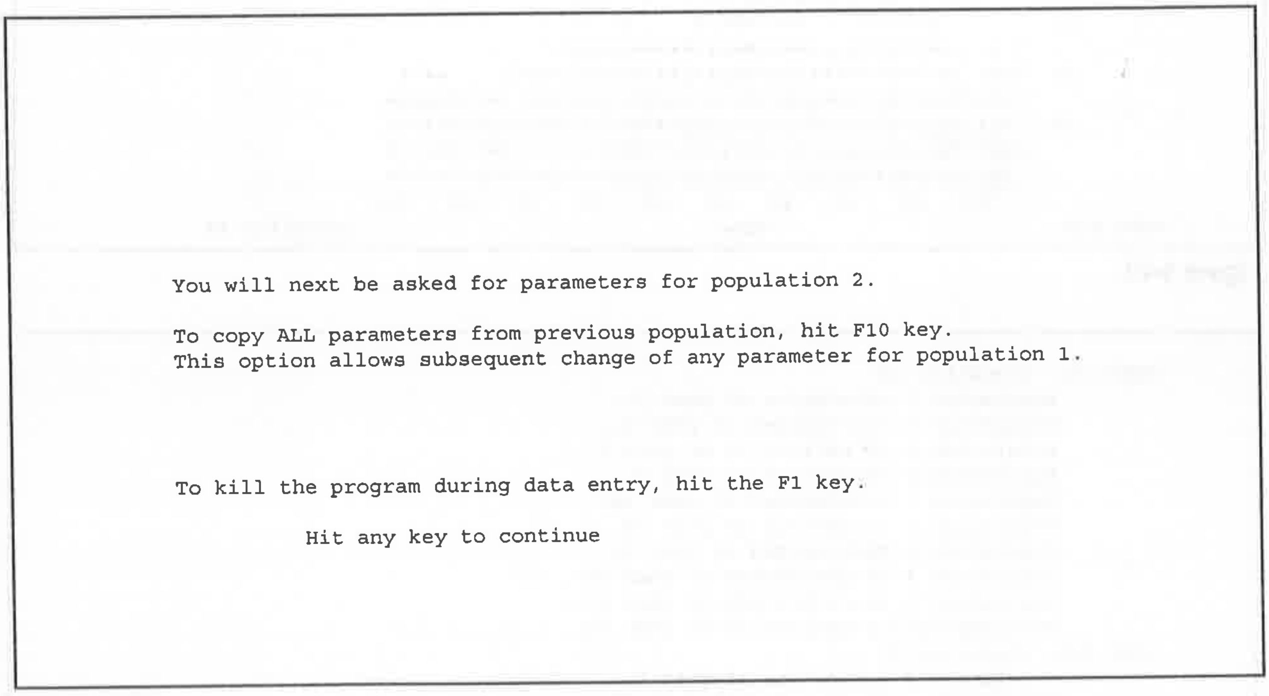
This question differs slightly from the similar question regarding harvest in that the last age class is the first year of adulthood as opposed to cumulative adult age classes. The difference results because harvesting selects any adult animal regardless of age, whereas in supplementation, VORTEX must assign an age class to each adult that is added. Adults supplemented to the population are always at the age of first breeding.

How many males age 1, 2 etc. added?

Again, all male age classes can be specifically supplemented.

If you have chosen more than one population, you must now go back to those populations and enter specific parameters (Figure 1-20). You may have already done this as you worked through the above questions. If you wish, you can hit the **F10** key to copy all parameters from the population currently highlighted by the cursor to all populations to the right. Doing so will take you back to the beginning of data entry for population 2 where you may wish to change only certain parameters while leaving the remainder identical to population 1. This will speed up data entry for your other populations. Repeat this process for all populations.

When all the data for all the populations have been input VORTEX will begin the simulation. Good luck!



```
You will next be asked for parameters for population 2.

To copy ALL parameters from previous population, hit F10 key.
This option allows subsequent change of any parameter for population 1.



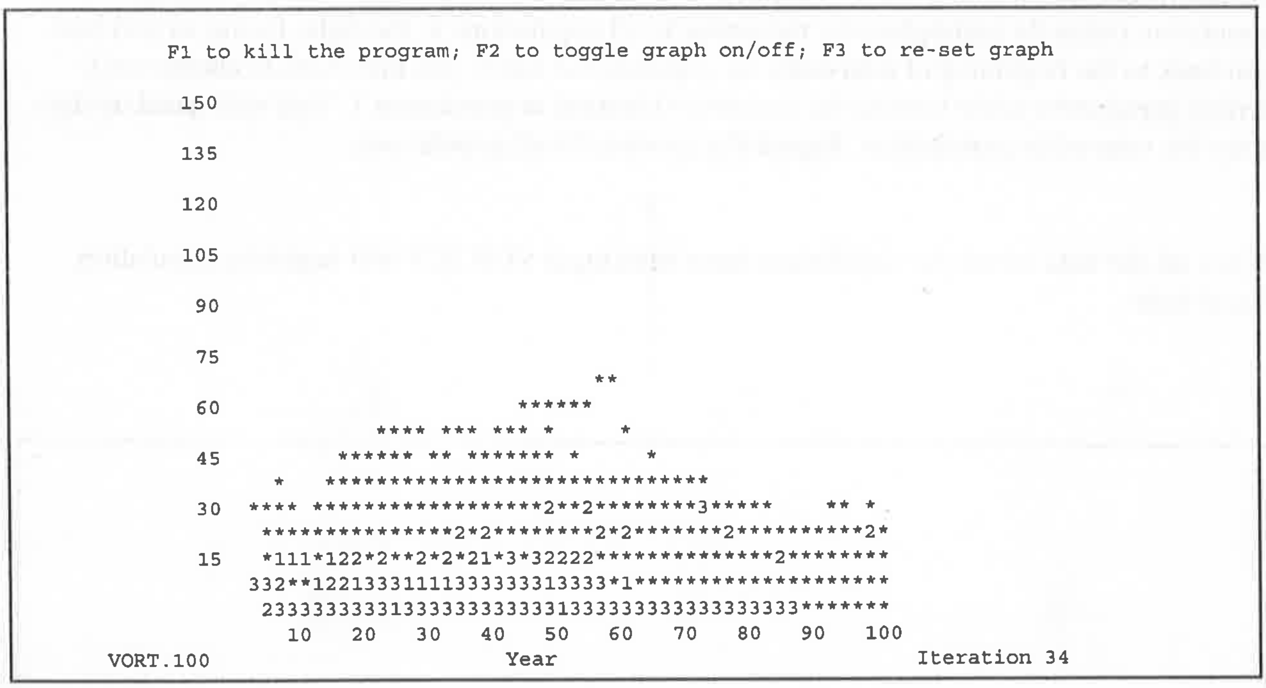
To kill the program during data entry, hit the F1 key.

          Hit any key to continue
```

Figure 1-20.

OUTPUT

While the VORTEX simulation is running, it will report (to the screen) whether each simulated population survives or goes extinct (and possibly is recolonized). There are two options for how you can see the progress of the simulations. If you chose (Figure 1-3) to see crude graphics of population size, then VORTEX will plot, with rather coarse resolution, the population size (and meta-population size if you are simulating multiple populations) at each reporting interval (Figure 1-21). If you chose not to see a run-time display of population size changes, VORTEX will simply show a dot on the screen for each year of the simulation (Figure 1-22). The run-time



```
     F1 to kill the program; F2 to toggle graph on/off; F3 to re-set graph
       150

       135

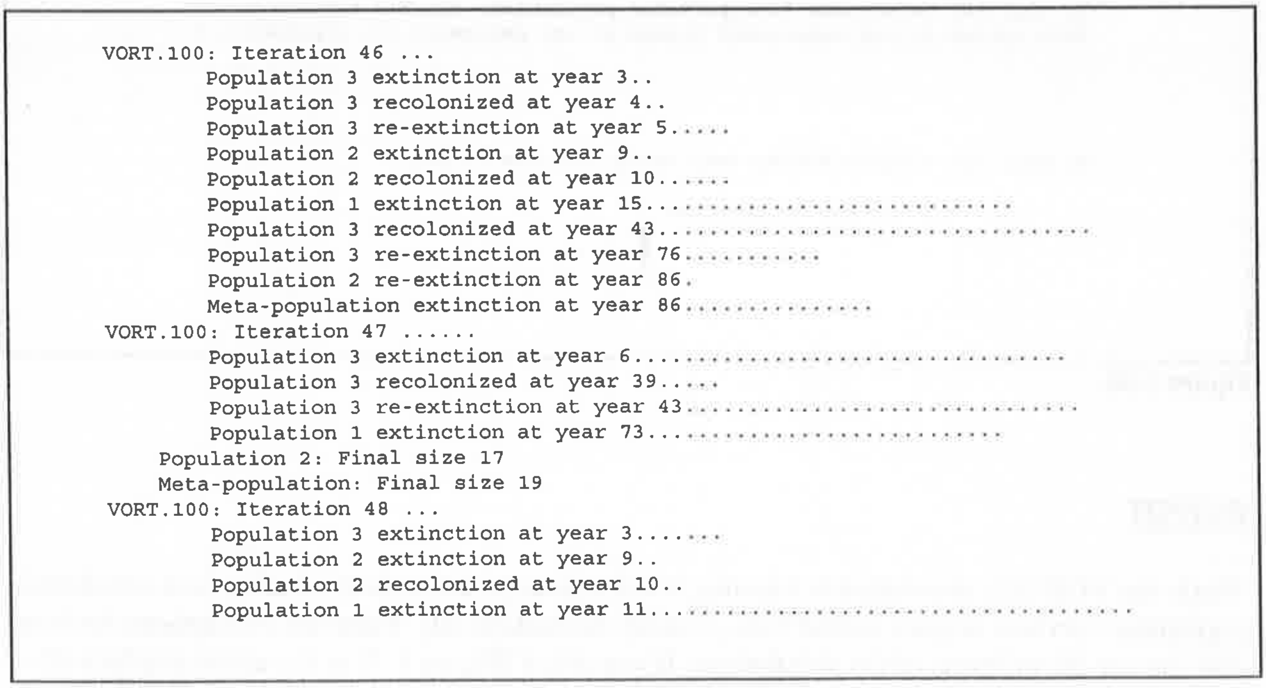
       120

       105

        90

        75
                                       **
        60                       ******
                      **** *** *** *     *
        45         ****** ** ******* *     *
              *   ******************************
        30  **** ******************2**2********3*****    ** *
             ***************2*2********2*2*******2**********2*
        15   *111*122*2**2*2*21*3*32222**************2********
            332**12213331111333333133333*1********************
             2333333333133333333333313333333333333333333*******
               10   20   30   40   50   60   70   80   90   100
VORT.100                        Year                                 Iteration 34
```

Figure 1-21.



```
VORT.100: Iteration 46 ...
        Population 3 extinction at year 3..
        Population 3 recolonized at year 4..
        Population 3 re-extinction at year 5.....
        Population 2 extinction at year 9..
        Population 2 recolonized at year 10......
        Population 1 extinction at year 15...................................
        Population 3 recolonized at year 43..........................................
        Population 3 re-extinction at year 76.............
        Population 2 re-extinction at year 86.
        Meta-population extinction at year 86..................
VORT.100: Iteration 47 ......
        Population 3 extinction at year 6.........................................
        Population 3 recolonized at year 39.....
        Population 3 re-extinction at year 43......................................
        Population 1 extinction at year 73..................................
    Population 2: Final size 17
    Meta-population: Final size 19
VORT.100: Iteration 48 ...
        Population 3 extinction at year 3.......
        Population 2 extinction at year 9..
        Population 2 recolonized at year 10..
        Population 1 extinction at year 11..............................................
```

Figure 1-22.

graphical display of population sizes is useful for visualizing how the simulated populations are faring, but the analysis will take a little longer when the population sizes are displayed during the simulation. The screen graphics can be toggled on/off by pressing the **F2** key at any time during the simulation. If you are running many iterations, the screen display of population sizes quickly becomes so cluttered as to be quite unreadable. (It still nicely shows the range of results, however.) The display of population sizes can be cleared of previous iterations by pressing the **F3** key during the simulation.

The display on the screen will probably go by much too fast to be read, but don't worry: The VORTEX simulation creates an output file, optional data files, and optional screen graphics that can be viewed or printed.

SCREEN GRAPHICS

If, at the beginning of the input (Figure 1-3), you specified that you wanted data files produced for graphing, VORTEX will have created an output file called VORTEX.DAT that provides detailed data at regular time intervals (as specified by the user) for graphing, statistical analysis, or whatever.

The data included in VORTEX.DAT are:

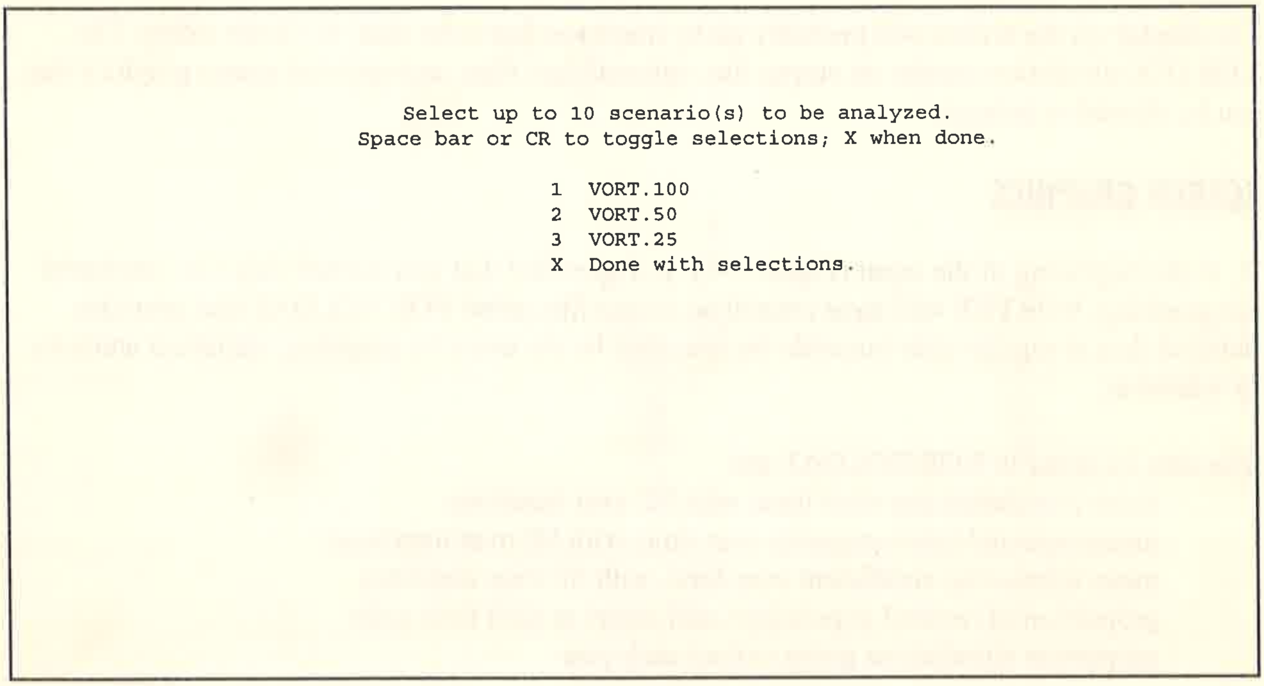
mean population size over time, with SE over iterations
mean expected heterozygosity over time, with SE over iterations
mean inbreeding coefficient over time, with SE over iterations
proportion of iterated populations still extant at each time point
proportion simulations going extinct each year

If you asked in addition for data from every iteration, then VORTEX will also have produced a file, NVORTEX.DAT, which contains the population size of each iteration over time. Note: the NVORTEX.DAT file is only created if you requested results from each run. The other statistics are all averaged across iterations (runs).

The output files are ASCII text files and can be imported into almost any spreadsheet, statistical, or graphics program. The data will be columns separated by commas, and there are header labels that identify the simulation run and the output data. If any of the output files existed before VORTEX ran, the new data will be appended to the old files. Thus, output files can get rather large if you are running many simulations and you do not rename the files, but you will not lose old data.

Select up to 10 scenarios to be analyzed. (Figure 1-23)

If you requested data files for graphing, and if data were entered via the keyboard, rather than from an input file, VORTEX will at the end of the simulation give you the option of seeing graphs of results on the screen. First VORTEX lists the analyses (by the label you gave for each output file) that are currently residing in the VORTEX.DAT file. You can select results from up to 10 analyses for graphing. Toggle your selections for which analyses to graph by typing the number that precedes a desired scenario or moving the cursor to a scenario, and then pressing either the **Space** or **Enter** key. Selected scenarios will be highlighted. When you are done making the selections, select **X** to move on to the next screen. (This will happen automatically if you have chosen 10 scenarios.)



```
                    Select up to 10 scenario(s) to be analyzed.
                 Space bar or CR to toggle selections; X when done.

                             1  VORT.100
                             2  VORT.50
                             3  VORT.25
                             X  Done with selections.
```

Figure 1-23.

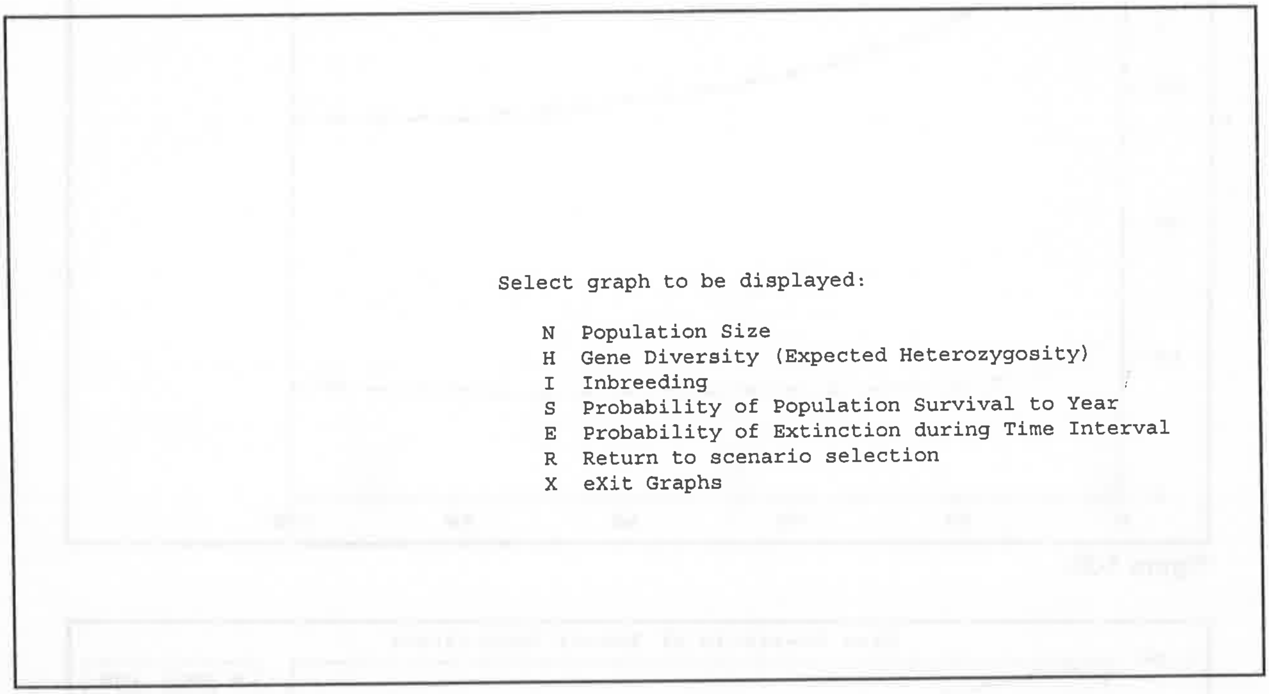
The option for graphical display of results on the screen is disabled if you entered input parameters via an input file, as it is assumed that the analyses will run unattended. However, files (VORTEX.DAT and NVORTEX.DAT) with output data for later graphing can still be produced. These output data will be available for screen graphics if a subsequent analysis is run with keyboard entry of input values.

Select graph to be displayed: (Figure 1-24)

Now select which kind of summary statistics you wish to see graphed. Your choices are:

Population size (Figure 1-25)
Gene Diversity or Expected Heterozygosity (Figure 1-26)
Inbreeding (Figure 1-27)
Probability of Population Survival to each Time Interval (Figure 1-28)
Probability of Extinction during each Time Interval (Figure 1-29)

Indicate your selection by moving to the desired graph and pressing the **Enter** key, or by typing the letter (`N`, `H`, `I`, `S`, or `E`) corresponding to the type of graph. After viewing the graph, press any key to go back to the graph selection screen (Figure 1-24). When you are done viewing graphs, press `R` if you wish to select a different set of scenarios to be viewed, or press `X` to exit the graph viewing mode.



```
Select graph to be displayed:

   N  Population Size
   H  Gene Diversity (Expected Heterozygosity)
   I  Inbreeding
   S  Probability of Population Survival to Year
   E  Probability of Extinction during Time Interval
   R  Return to scenario selection
   X  eXit Graphs
```

Figure 1-24.

You can customize what graphs you can display by editing the VORTEX.DAT file. Use a text editor to do this, but be sure to save the file as an ASCII (DOS) text file. You may also wish to "capture" the screen graphs for later printing or inclusion in other documents. Various software programs exist for doing this (e.g., the GRAB command supplied with WordPerfect was used to capture Figures 1-25 through 1-29 for this manual). Because the VORTEX graphs use various colors and symbol types, however, often the image that is captured for printing is not nearly as easy to read as was the graph on the screen. For example, the graphs in this manual (Figures 1-25 through 1-29) were much clearer on the screen than shown here.

These screen graphics can also be displayed for previous VORTEX analyses by running the program VORTGRAF.

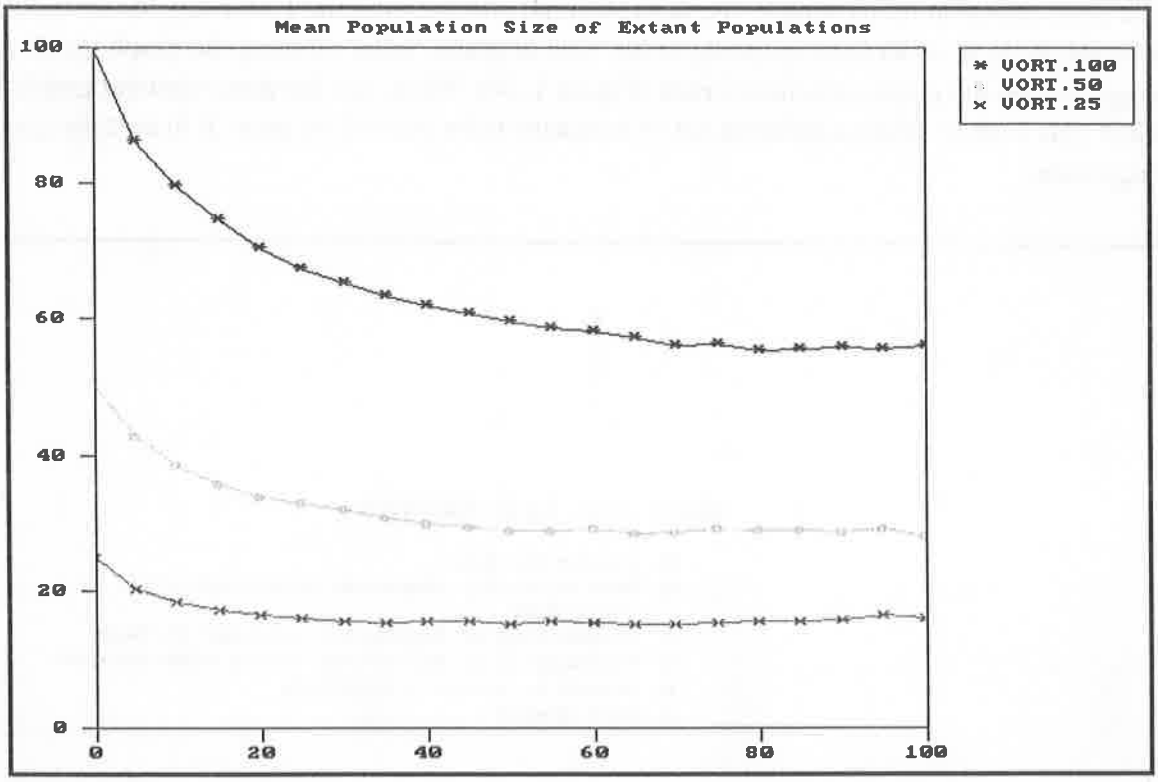


Figure 1-25.

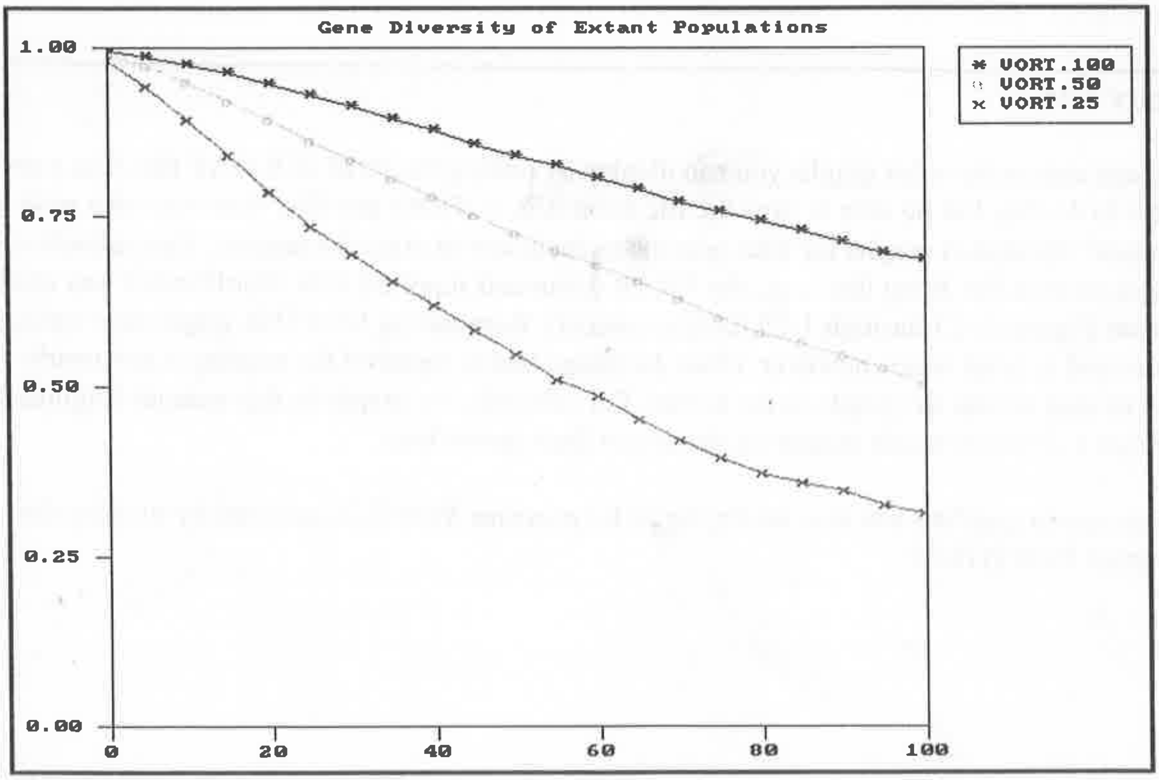


Figure 1-26.

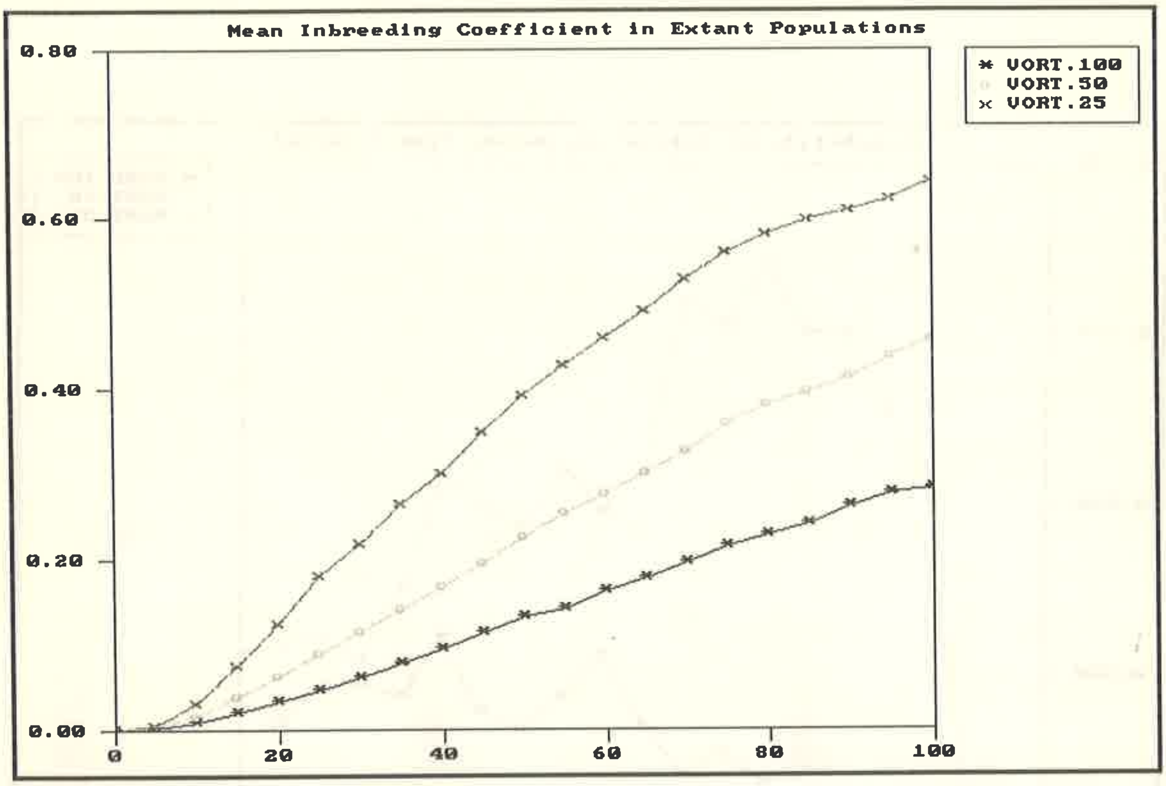


Figure 1-27.

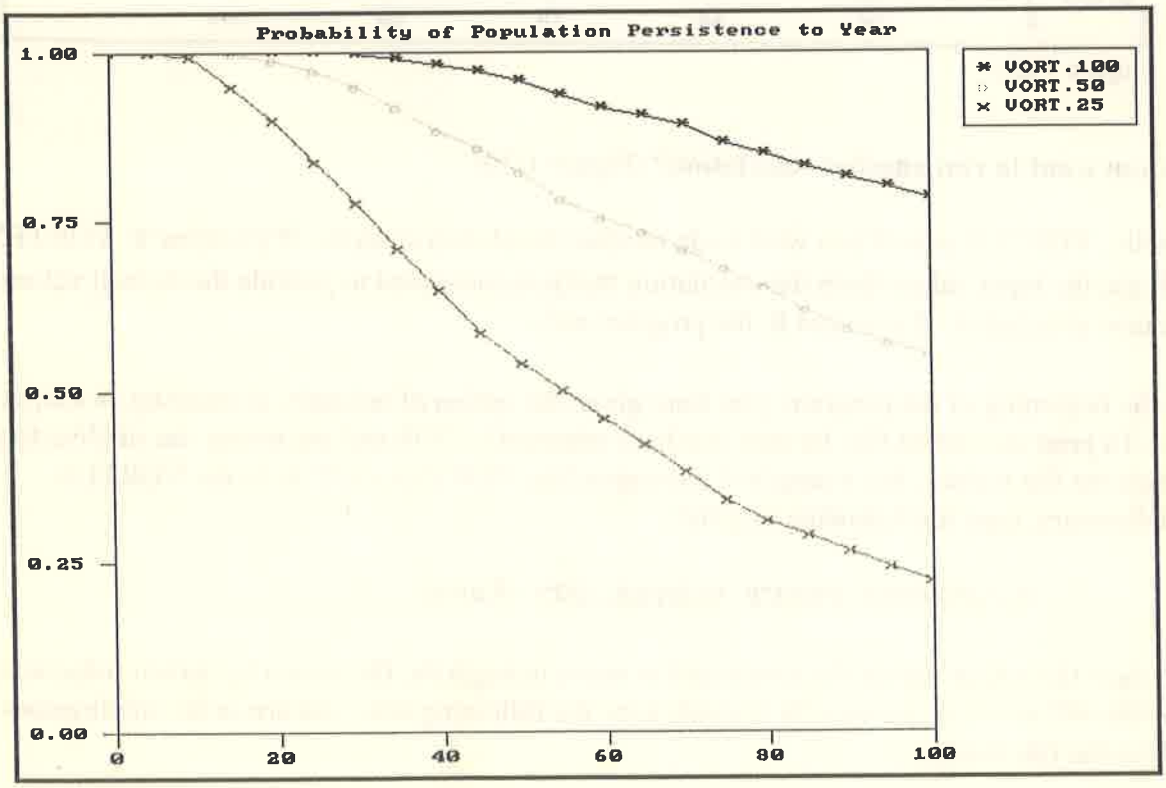


Figure 1-28.

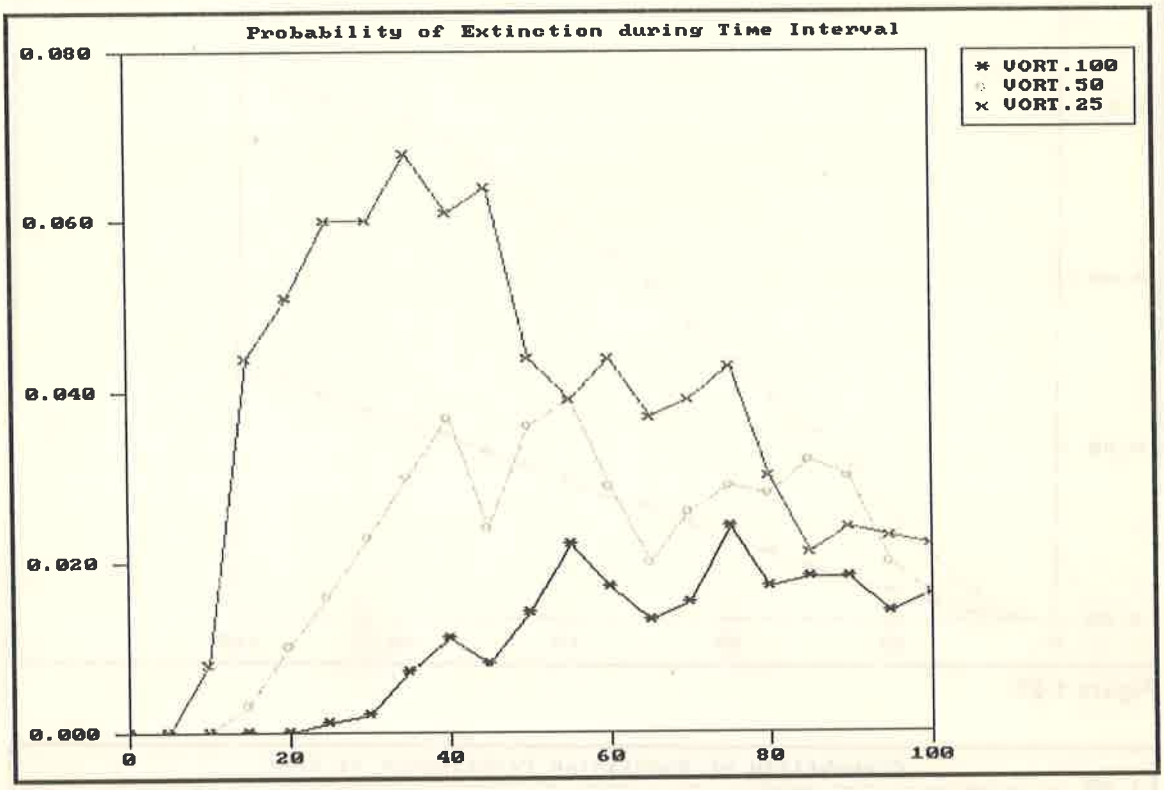


Figure 1-29.

Do you want to run another simulation? (Figure 1-30)

Finally, VORTEX asks if you wish to do another simulation analysis. If you type **Y**, VORTEX will use the input values from the simulation that just completed to provide the default values for the next simulation. If you type **N**, the program ends.

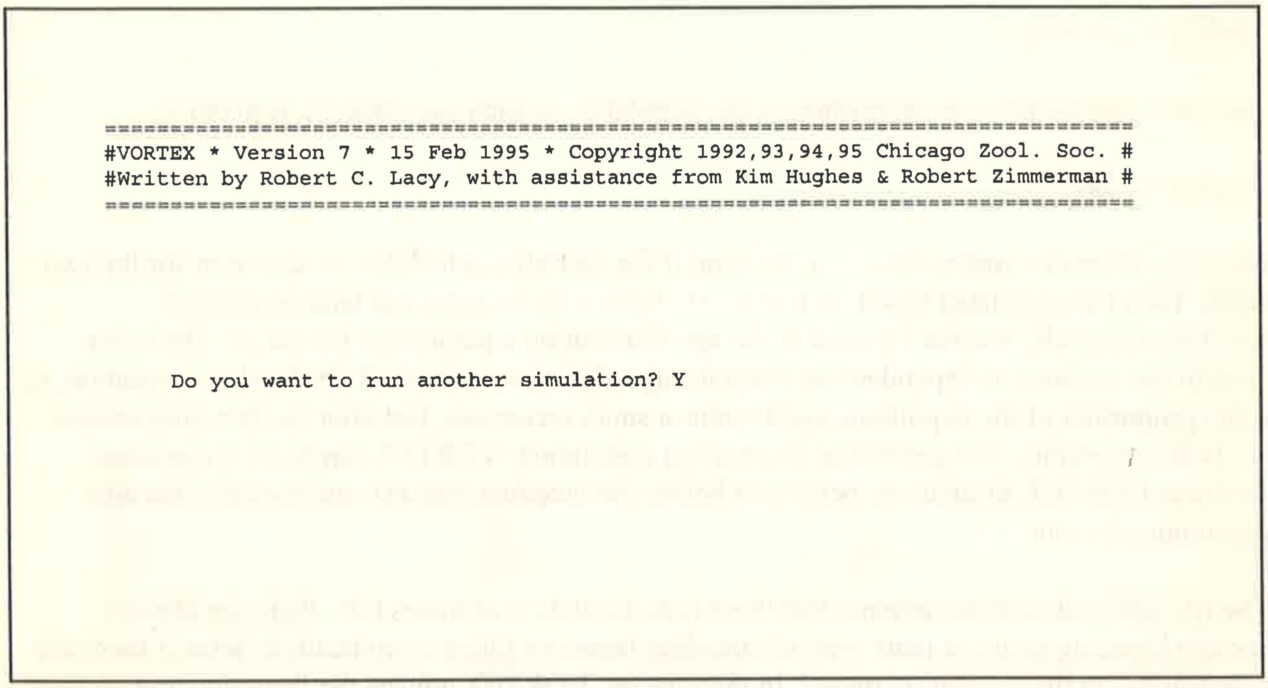
At the beginning of the program, you were given the option of uniquely identifying an output file. To print the output file, be sure you have returned to DOS and are within the subdirectory in which the file resides. For example if the output file, VORTEX.OUT, is in the VORTEX subdirectory, type the following to print:

```
C:\VORTEX>PRINT VORTEX.OUT (Enter)
```

To view the output file on the screen and to move through the file screen by screen (otherwise the file will scroll by too rapidly to read), type the following once you are in the subdirectory where the file resides:

```
C:\VORTEX>TYPE VORTEX.OUT |MORE (Enter)
```

Note the use of the vertical bar or pipe (|) preceding the word MORE.



```
================================================================================
#VORTEX * Version 7 * 15 Feb 1995 * Copyright 1992,93,94,95 Chicago Zool. Soc. #
#Written by Robert C. Lacy, with assistance from Kim Hughes & Robert Zimmerman #
================================================================================



     Do you want to run another simulation? Y
```

Figure 1-30.

VORTEX OUTPUT: TECHNICAL NOTES

Deterministic life table calculations

Before running the simulation, VORTEX performs a standard life table analysis (see Pielou 1977; or almost any population ecology text) to determine the deterministic mean population growth rate (r, the exponential growth rate; or lambda, the annual multiplicative growth rate), the mean generation time for females and males, and the stable age distribution. These calculations will provide accurate long term averages, if stochastic variation (due to demographic stochasticity, environmental variation, catastrophes, and inbreeding effects) is minimal. Life table analyses implicitly assume that age-specific birth and death rates are constant through time; they yield over-estimates of long-term population growth if there is any variation in demographic rates.

Population growth rate, r, is calculated by solving:

$\Sigma(l_x m_x e^{-rx}) = 1$, in which l_x and m_x are the age-specific mortality and fecundity rates for age class x to x+1, and the summation is over all age classes.

Lambda is given by e^r.

The stable age distribution proportion of the population at each age class, c_x, is given by:

$c_x = (l_x e^{-rx}) / \Sigma(l_x e^{-rx})$.

The calculations for males are a bit confusing if the mortality schedules are different for the two sexes. Then r is calculated based on female life history tables (because females control population growth), but the l_x's used in the age distribution equation are for males. The exact form of the equation is dependent on when the age classes are censused. In the above equation, c_0 is the proportion of the population aged 0 plus a small increment, just after the breeding season but before mortality. For generating the starting population, VORTEX omits the 0 age class (because VORTEX simulations begin just before the breeding season), and re-scales the age distribution to sum to 1.

The life table calculations assume that there is no limitation of mates (i.e., there are always enough breeding males to mate with all breeding females). Other complications arise if there are catastrophes in the simulation model. In those cases, VORTEX adjusts the fecundity and mortality rates to account for the effect of catastrophes, averaged across years.

It is important to look at the deterministic projections of population growth for any analysis. If $r < 0$, then the population is in deterministic decline (deaths outpace births), and will go extinct even in the absence of any stochastic fluctuations. The difference between the deterministic population growth rate and the growth rate resulting from the simulation (see below) can give an indication of the importance of stochastic factors as threats to population persistence.

Simulation results

Following the stochastic simulation, VORTEX provides a number of statistics that summarize the demographic and genetic stability projected for the population, including:

- probability of population persistence to each time interval,
- mean population size (with SD and SE across iterations) of those simulated populations that are still extant,
- mean "expected heterozygosity" (or "gene diversity") remaining in the extant populations at each time interval,

- mean "observed heterozygosity" (= 1 - mean inbreeding coefficient) remaining in extant populations at each time,
- mean number of founder alleles remaining within the extant populations at each time interval (each founder starts with two unique alleles at the beginning of each simulated population),
- and, if the Recessive Lethals option of inbreeding depression was chosen,
- mean number of recessive lethal alleles remaining (each founder starts with one recessive lethal),
- frequency of lethal alleles in the extant populations (starts at 0.50).

VORTEX also gives, at the end of the output, the mean and median times to population extinction, the final age-sex composition of the extant populations, and the mean population growth rate experienced by the simulated populations. VORTEX defines extinction as occurring if there are no individuals in the population, or only individuals of one sex (unless hermaphroditic). If harvest or supplementation was modeled, VORTEX will give the mean population growth rate separately for those years in which harvest or supplementation occurred and for those years in which there was no harvest or supplementation. If any recolonizations occurred, VORTEX will report the frequency of recolonization, the mean time to recolonization, and the frequency and mean time to re-extinction of population. If a meta-population with multiple subpopulations was modeled, VORTEX will give the above statistics for each subpopulation, for the meta-population, and as within-subpopulation averages.

VORTEX places one line of basic summary data from each analysis—including the predicted deterministic growth rate, r; the average population growth rate that resulted from the simulation, with its standard deviation across years and iterations; the probability of extinction over the time span of the simulation; the mean (and SD) population size for those simulated populations that survived; and the mean (and SD) expected heterozygosity for these extant populations—into a file, VORTEX.SUM. These summary statistics can then be easily imported into spreadsheet or word processing software for tabular presentation.

More detailed description of the output provided by VORTEX can be found in the *Wildlife Research* paper reprinted as Chapter 5 of this manual.

VORTEX Version 7 Notes for Macintosh™ Users

To a considerable extent, use of the Macintosh version of VORTEX is identical to the use of the MS-DOS version. Input screens, output files, and—most importantly—results should be identical. The same source code was used for MS-DOS and Macintosh compilations of the program, but we cannot guarantee that machine-dependent differences in implementation of the code will not lead to some differences in results. (Similarly, we cannot guarantee that VORTEX is free of all bugs, and will run on all MS-DOS computers.) The Macintosh version of VORTEX was compiled with Symantec's ThinkC compiler (Version 6).

The primary differences in the use of VORTEX on Macintosh vs. computers running MS-DOS are in the way in which the program is loaded on the system, special keys used for some functions, the ways in which output files might be viewed and printed on the two types of systems, and the lack of availability of screen graphics displaying output summaries on the Macintosh version. (We recognize the irony in this lack of graphics in the Mac version -- considering that Macintosh has better graphical capabilities than does MS-DOS. We also recognize that mouse capabilities would be handy. But those are the drawbacks of having a Macintosh version produced by MS-DOS system programmers!)

LOADING VORTEX ON A MACINTOSH COMPUTER

1 Open the hard disk by double-clicking on its icon.
2 Place the distribution disk into the floppy drive.
3 Open (double click) the floppy drive.
4 Click on the **VORTEX** folder in the floppy drive and drag it to your hard disk.
5 Close the floppy drive and eject the distribution disk by dragging the drive icon to the Trash. Store the distribution disk in a safe place.

To start VORTEX running, open the **VORTEX** folder and double click on the **VORTEX** application icon. With a very few exceptions (see below), the use of VORTEX on a Macintosh is then identical to the use on a PC running MS-DOS, as described in the VORTEX manual.

If you run into problems with apparently insufficient memory to run VORTEX, increase the amount of memory given to the program at startup. Click (once) on the **VORTEX** application icon, and then use the Get Info dialogue box in the **File** menu of Finder to increase the memory available to the application. The default memory allocation is 4 MB.

KEYBOARD DIFFERENCES

Because some Macintosh keyboards lack some control keys used by MS-DOS, alternate keystrokes have been defined as the equivalent of the missing function and page keys.

MS-DOS key	Mac equivalent	Purpose
F1	CTRL-D	Exit program during data entry
F10	CTRL-V	Copy input data to next population
PgUp	SHIFT-UP	Move to previous input window
PgDn	SHIFT-DN	Move to next input window

VIEWING OUTPUT FILES

The output files (e.g., VORTEX.OUT, VORTEX.SUM, VORTEX.DAT, and NVORTEX.DAT) can be viewed using your favorite word processor.

GRAPHICS

A graph displaying the population size during a simulation is available as an option in the Macintosh version of VORTEX, as it is in the PC version. However, the ability to toggle on/off the run-time display of population size (with the **F2** key), and to reset the screen graph (**F3** key) is disabled in the Macintosh version.

If the user requests data files to be produced for graphics, VORTEX will create the file VORTEX.DAT and, optionally, NVORTEX.DAT. These files contain results that can then be imported to other programs in order to produce graphical displays or for statistical analysis. The option provided in the MS-DOS version to view graphs on the screen at the end of the simulation (Figures 1-25 through 1-29 in the manual) is NOT available to Mac users.

SUPPORT

We would like to hear about any problems (or just interesting applications) you have with the Macintosh version of VORTEX. Unfortunately, however, we cannot provide the level of support to Macintosh users that is provided to MS-DOS users (and that is not a lot). We can usually resolve any problems arising from bugs in the code, but we may not be able to assist with machine-dependent problems arising from which flavor of Macintosh and which version of the operating system you have available.

VORTEX

A Stochastic Simulation of the Extinction Process

Version 7

Chapter 2:

An Overview of Small Population Biology

An Overview of Small Population Biology

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Department of Zoological Research
National Zoological Park
Washington, DC, USA

The primary objective of single-species conservation programs is to reduce the risk of population extinction. A first step in doing this is to identify those factors that can potentially cause extinction in the population. The most fundamental threat is, of course, declining population size. If a population is declining in numbers, and no action is taken to reverse the trend, then extinction is imminent. However, even if a small population is not declining or even if it is increasing, its fate is uncertain. Small populations arc challenged by a number of factors that increase the likelihood of the population going extinct simply because the population is small.

Challenges to Small Populations

Challenges to small populations can be categorized as intrinsic (random variation of genetic and demographic events within the population occurring withhout reference to environmental events) or extrinsic (environmental events acting on the genetics and demography of a population)

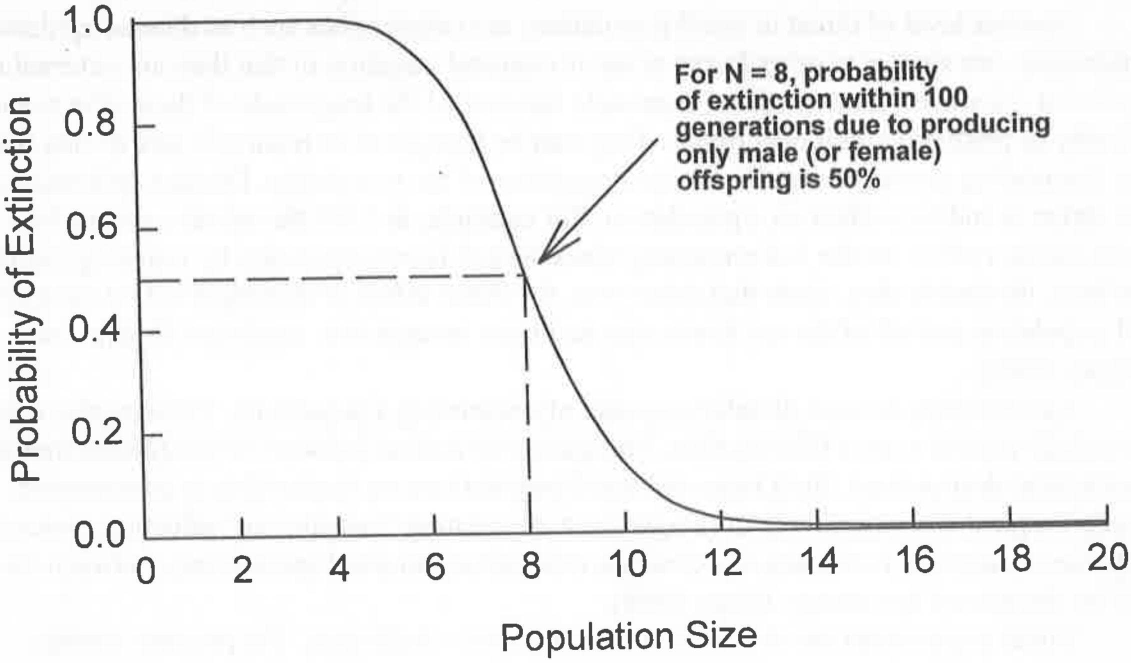

Figure 2-1. Demographic variation. The probability of population extinction in 100 generations due solely to producing only one sex of offspring in any single generation.

(Hedrick and Miller 1992). At the most basic level, the level of the individual, an intrinsic challenge to the population is demographic variation. Demographic variation is the normal variation in the population's birth and death rates and sex ratio caused by random differences among individuals in the population. The population can experience fluctuations in size simply by these random differences in individual reproduction or survival. These randomly caused fluctuations can be severe enough to cause the population to go extinct. For example, one concern in extremely small populations is the possibility that all individuals born into the population during one generation are of one sex, resulting in the population going extinct. Figure 2.1 illustrates the probability of this event occurring over a 100 generation period in populations of different size. There is a 50% chance of extinction due to a biased sex ratio in a population of size 8 sometime during this period.

Similar consequences could result from the coincidental effects of high death rates or low birth rates. However, these risks are practically negligible in large populations. In general, the effect of any one individual on the overall population's trend is significantly less in large populations than small populations. As a result, demographic variation is a relatively minor challenge in all but very small populations (i.e., less than twenty animals).

A more significant extrinsic threat to small populations is environmental variation. Variation in environmental conditions clearly impacts the ability of a population to reproduce and survive. Populations susceptible to environmental variation fluctuate in size more than less susceptible populations, increasing the danger of extinction. For example, reproductive success in the endangered Florida snail kite (*Rostrhamus sociabilis*) is directly affected by water levels, which determine prey (snail) densities: nesting success rates decrease by 80% during years of low water levels. Snail kite populations, as a result, are extremely unstable (Beissinger 1986).

Another level of threat to small populations are catastrophes such as disease epidemics. Catastrophes are similar to other forms of environmental variation in that they are external to the population. However, they are listed separately because of the magnitude of their effects and the difficulty of predicting their occurrence. They can be thought of as relatively rare events that can have devastating consequences for a large proportion of the population. Disease epidemics can have direct or indirect effect on a population. For example, in 1985 the sylvatic plague had a severe indirect effect on the last remaining black-footed ferret population by reducing the ferret's prey base, the prairie dog. Later that same year, the direct effect of distemper killed most of the wild population and all of the six ferrets that had been brought into captivity (Thorne and Belitsky 1989).

Catastrophes are rare disasters capable of decimating a population. Catastrophic events can include natural events (floods, fires, hurricanes) or human-induced events (deforestation or other habitat destruction). Both large and small populations are susceptible to catastrophic events. Tropical deforestation is the single most devastating "catastrophe" affecting present rates of species extinction. Estimates of extinction rates among tropical species vary between 20 and 50% by the turn of the century (Lugo 1988).

Small populations are also susceptible to genetic challenges. The primary genetic consideration is the loss of genetic variation. Every generation, the genes that are passed on to offspring are a random sample of the genes of the parents. In small populations, each random sample of genes is a small sample and represents only a fraction of the genes of the parental generation. Some of the genetic variation present in the parents may not, just by chance, get passed on to the offspring. This genetic variation is then lost to the population. This process is called genetic drift because the genetic characteristics of the population can drift or vary over time. In small populations, genetic drift can lead to rapid loss of genetic variation—the smaller the population, the more rapid the loss of variation.

Conservation programs include the maintenance of genetic diversity as a primary goal for several reasons. If species are to survive over the long term, they must retain the ability to adapt to changing environments. Since the process of natural selection requires the presence of genetic variation, conservation strategies must include the preservation of gentic diversity for long-term survival of species. In addition to long-term evolutionary considerations, the presence of genetic diversity has been shown to be important for maintaining the fitness of the population. A growing number of studies show a general, but not universal, correlation between genetic diversity and various traits related to reproduction, survival and disease resistance (Allendorf and Leary 1986; Mitton 1993). Individuals with lower levels of genetic variation often have higher mortality rates and lower reproductive rates than individuals with greater diversity.

Inbreeding (matings between relatives) also causes populations to lose genetic diversity. All the animals in small populations quickly become related. An offspring produced from related parents is inbred and can receive the same ancestral allele through both its mother and father. Inbred individuals are therefore more homozygous than non-inbred individuals and they have lower levels of genetic diversity than animals born to unrelated parents.

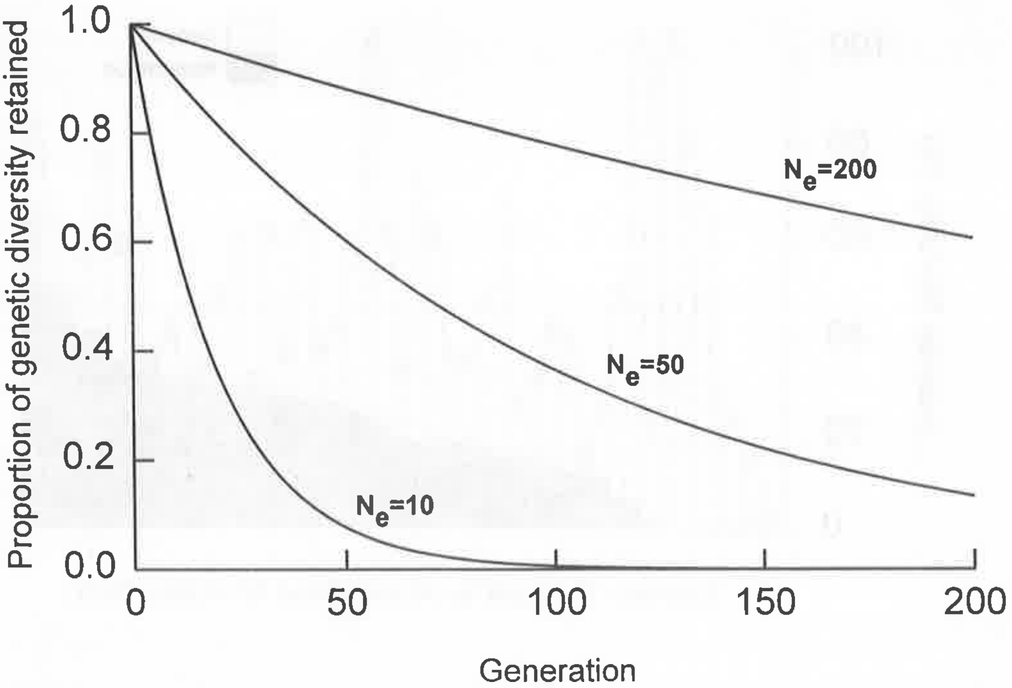

Figure 2-2. Loss of genetic diversity over 200 generations in populations with different effective sizes (N_e).

The loss of genetic variation in populations of different size is shown in Figure 2-2. The rate of loss is a function of the effective size of the population, N_e: the proportion of diversity lost each generation is $1/(2N_e)$. Technically, a population's effective size is the size of an ideal population that loses genetic diversity at the same rate as the real population. There is an extensive literature on how to estimate a population's effective size (Lande and Barrowclough 1987); however, the number of animals contributing to the breeding pool each generation can be used as a very rough estimate of the effective size. The effective size of a population is therefore much less than the actual number of animals; estimates suggest that Ne is often only 10 to 30% of the total population. Seemingly large populations will lose significant levels of genetic diversity if their effective sizes are small.

Data on the effects of inbreeding in exotic species also show the importance of maintaining genetic diversity. Numerous studies have shown that inbreeding can significantly reduce reproduction and survival in a wide variety of wildlife (Ralls and Ballou 1983; Wildt et al. 1987; Lacy et al. 1993a; Figure 2-3). Inbreeding depression results from two effects: 1) the increase in homozygosity allows deleterious recessive alleles in the genome to be expressed (whereas they are not in non-inbred, more heterozygous individuals); and 2) in cases where heterozygotes are more fit than homozygotes simply because they have two alleles, the reduced heterozygosity caused by inbreeding reduces the fitness of the inbred individuals (a phenomenon known as overdominance). In both cases, the loss of genetic variation due to inbreeding has detrimental effects on population survival. Small, isolated populations, with no migration from

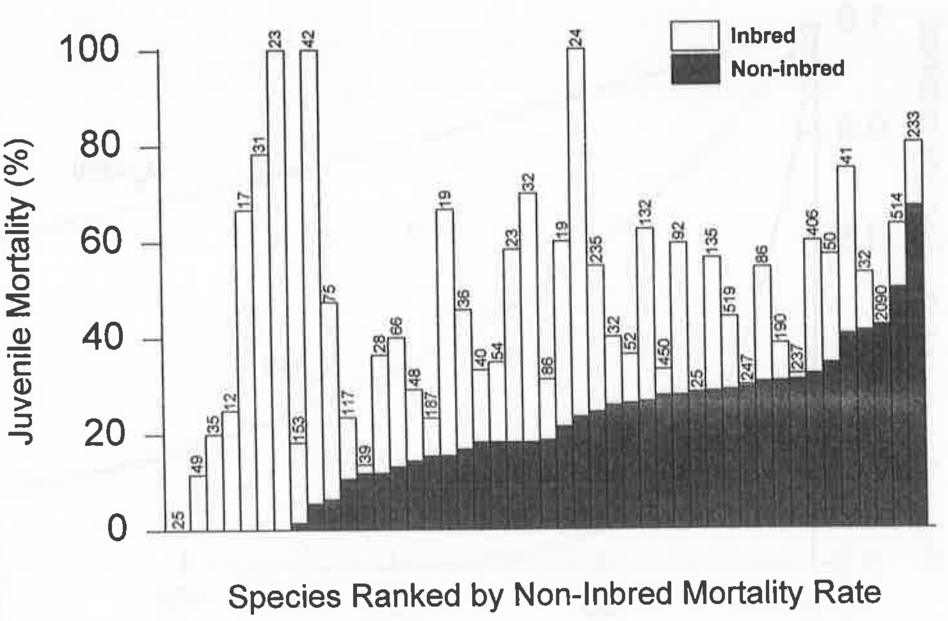

Figure 2-3. Effects of inbreeding on juvenile mortality in 45 captive mammal populations (from Ralls and Ballou 1986).

other populations, lose genetic diversity and become increasingly inbred over time. Their long-term survival potential is doubly jeopardized since they gradually lose the genetic diversity necessary for them to evolve and their short-term survival is jeopardized by the likely deleterious effects on survival and reproduction.

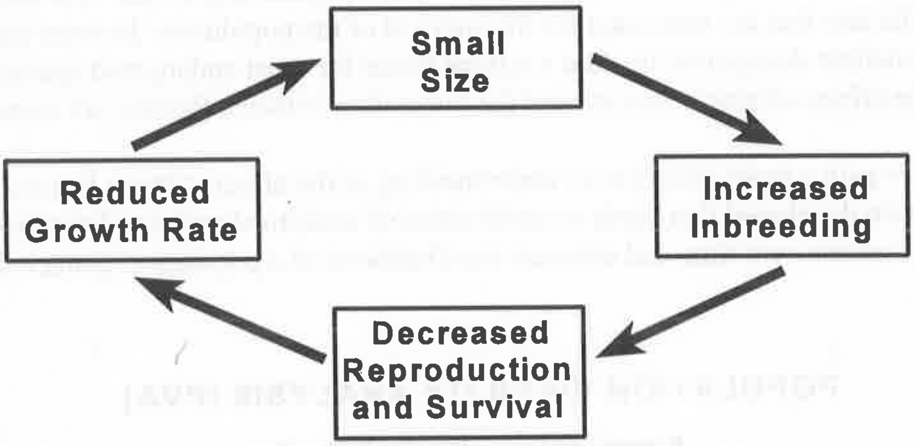

Figure 2-4. The "extinction vortex" caused by negative feedback effects of inbreeding in small populations.

The genetic and demographic challenges discussed above clearly do not act independently in small populations. As a small population becomes more inbred, reduced survival and reproduction are likely: the population decreases in size. Inbreeding rates increase and because the population is smaller and more inbred, it is more susceptible to demographic variation as well as disease and severe environmental variation. Each challenge exacerbates the others, resulting in a negative feedback effect termed the "extinction vortex" (Gilpin and Soulé 1986). Over time, the population becomes increasingly smaller and more susceptible to extinction (Figure 2-4).

Population Viability Analysis

Many of the challenges facing small populations are stochastic and result from random, unpredictable events. Many can generally be assumed to decrease the likelihood of long-term survival of the population. However, because of their stochastic nature, their exact effects on population extinction and retention of genetic diversity cannot be predicted with total accuracy. For example, although inbreeding depression is a general phenomenon, its effects vary widely between species (Figure 2-3) and it is not possible to precisely predict how any one population will respond to inbreeding.

Nevertheless, conservation strategies that address these unpredictable issues of extinction and loss of genetic diversity must be developed and implemented. The process that has been developed over recent years to assess extinction probabilities and loss of genetic diversity is called population viability analysis, or PVA (Soulé 1987). PVA is defined as a systematic evaluation of the relative importance of factors that place populations at risk. It is an attempt to identify those factors that are important for the survival of the population. In some cases, this may be easy—habitat destruction is often a critical factor for most endangered species. But at other times, the effects of single factors, and the interaction between factors, are more difficult to predict.

To try to gain a more quantitative understanding of the effect of these factors, computer models have been developed that apply a combination of analytical and simulation techniques to model the populations over time and estimate the likelihood of a population going extinct and its loss of genetic variation. The model is first provided with information describing the life-history characteristics of the population. Depending on the model used, this includes data on the age of first reproduction, litter size distribution, survival rates, mating structure and age distribution as well as estimates of the variation associated with each of these variables. A number of different external factors may also be considered. These may include levels of environmental variation, change in carrying capacity, and severity of inbreeding depression. Models also allow consideration of the threats facing the population: probabilities of catastrophes and their severity, habitat loss, and disease epidemics (Figure 2-5). The models use the life-history variables, the

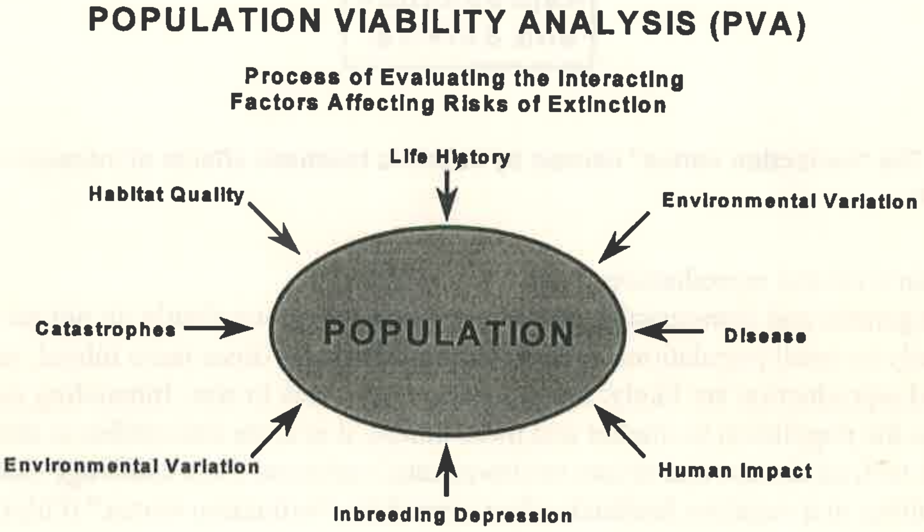

Figure 2-5. Population viability analysis (PVA) models the effects of different life-history, environmental, and threat factors on the extinction and retention of genetic diversity in single populations.

external factors and the potential threats to project the population into the future, measuring the level of genetic variation that is retained over time and recording if and when the population goes extinct (population size is reduced to zero). The simulations are repeated, often thousands of times, to provide estimates of the statistical variation associated with the results. The probability of extinction at any given time is measured as the number of simulations that the population became extinct within the specified time interval, divided by the total number of simulations run (Figure 2-6). The levels of genetic variation are recorded as the percent of the original heterozygosity and the number of original founder alleles retained in the population at any particular point in time.

The true value of population viability models in general, and the VORTEX model in particular, is not in trying to examine the effects of all variables in the population simultaneously. The interactions between these many factors is too complex to attempt to interpret the results of population projections based on more than just a few of these considerations. We can gain far more insight into the dynamics of the population by examining only one or two factors at a time—and choosing those factors that we believe have an impact on the population and ignoring those that don't.

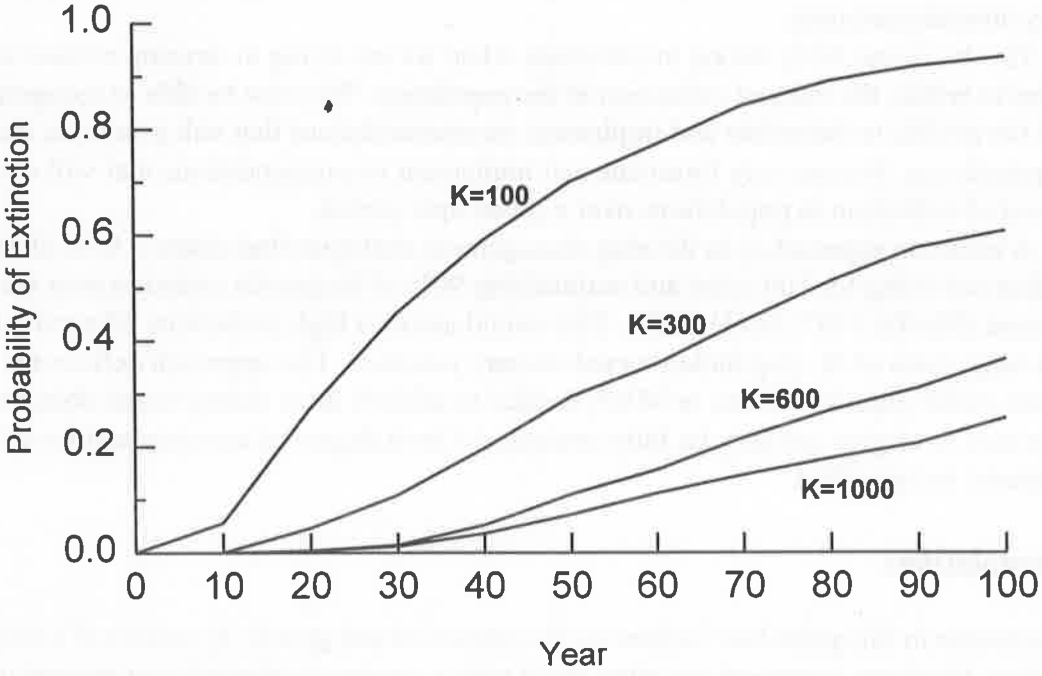

Figure 2-6. Example of population extinction results from the VORTEX model. The cumulative probability of extinction over time is shown for four populations with different carrying capacities.

The primary use of the model in developing conservation strategies is its use in conducting "what if?" analyses. For example, "what if" survival were decreased in the wild population as a result of a disease outbreak? How would that affect the extinction of the population and the retention of genetic diversity? These "what if" analyses can also be used to evaluate management recommendations. For example, how would the probability of population extinction change if the carrying capacity of the reserve holding the animals were increased by 10%?

Because the models don't examine all factors potentially contributing to extinction, the results usually underestimate a population's probability of extinction. However, it is important to stress that the purpose of PVA is not to estimate exact extinction probabilities but to identlfy the relative importance of the various factors being considered and to evaluate the effect of a range of management recommendations on the survival of a population.

Implications of PVA for Management Goals

The concepts of population extinction and loss of genetic diversity are based on probabilities rather than on certainties. The results of PVA models provide us with information on the probability of extinction given certain assumptions about the biology and current status of the population. As a result, we cannot predict or guarantee what will happen to these populations with any absolute certainty.

This has some fairly strong implications when we are trying to develop conservation strategies to reduce the risks of extinction in the population. We must be able to recognize that we will not be able to formulate and implement recommendations that will guarantee the survival of any population. We can only formulate and implement recommendations that will decrease the likelihood of extinction in populations over a given time period.

A common approach is to develop management strategies that assure a 95% chance of the population surviving for 100 years and maintaining 90% of its genetic variation over the same time period (Shaffer 1987; Soulé 1986). This would assure a high probability of survival and retain a large share of the population's evolutionary potential. This approach defines the minimum viable population size, or MVP, needed to achieve these management objectives. Management strategies can only be fully evaluated if both degree of certainty and time frame for management are specified.

Metapopulations

The discussion to this point has focused on the extinction and genetic dynamics of a single population. However, managers are often faced with a species distributed over several interacting populations. When this is the case and animal movement (migration) between populations is high enough that the dynamics of any single population is affected by the dynamics of other nearby populations, the group of interacting populations is called a metapopulation (Figure 2-7). The understanding of metapopulation dynamics has become increasingly important for the development of conservation strategies (Gilpin 1987; see also Gilpin and Hanski 1991 and Hastings and Harrison 1994 for reviews of metapopulation theory). Metapopulation management focuses on the spatial distribution of the population and how that influences both the genetic and

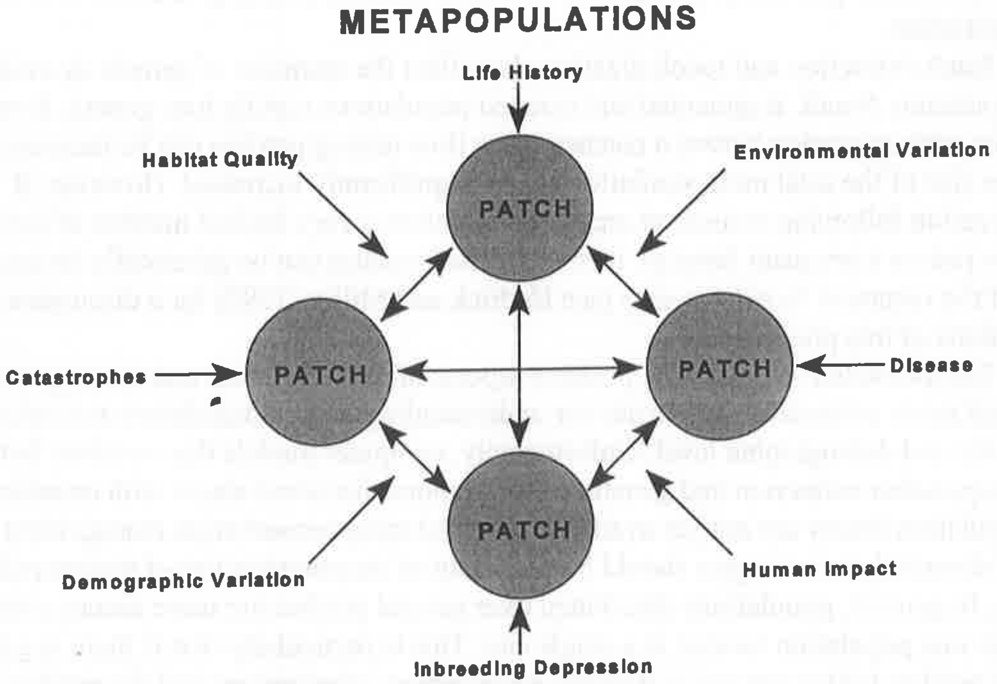

Figure 2-7. The interaction between population "patches" results in a metapopulation structure. Conservation strategies must consider the spatial distribution of patches and its effect on correlated extinctions and recolonization between patches.

demographic dynamics of the system. The metapopulation system can be thought of as a group of subpopulations, or "patches", of different size and separated from each other by varying distances, with some patches periodically going extinct and being recolonized by migrants from other patches. The most important conservation considerations are rates of patch extinction and the rate of recolonization between patches.

As has been discussed above, the extinction dynamics of any single patch is affected by any number of factors including size of population, rate of population recovery following a population decline, etc. From a metapopulation perspective, the simplest level is when patch extinction rates are not correlated with each other: the probability of extinction of any one patch is independent of any other patch. Environmental variation and catastrophes increase the extinction correlation between patches and this increases the likelihood of the entire metapopulation becoming extinct. Consequently, considerations of the spatial distribution between patches, and what that means in terms of how similarly they react to environmental variation and catastrophes, is an important part of developing management strategies.

On the other side of the coin is the effect of spatial distribution on recolonization rates between patches. The closer patches are to each other, the higher the probability of a patch being recolonized following an extinction by migrants from a neighboring patch. Thus, distance between patches is positively correlated with recolonization and long-term survival of the metapopulation.

Patch extinction and recolonization also affect the retention of genetic diversity in the metapopulation. Small, fragmented and isolated populations rapidly lose genetic diversity. However, with migration between patches, gene flow among patches can be increased and the effective size of the total metapopulation can be significantly increased. However, if recolonization following extinction repeatedly involves a very limited number of individuals (i.e., one pair or a pregnant female), then individual patches can be genetically invariant as a result of the recurrent founder events (see Hedrick and Miller (1992) for a discussion of the implications of this phenomenon).

The interaction between the positive aspects of recolonization and the negative effects of correlated patch extinction complicate our understanding of metapopulation dynamics, both at the genetic and demographic level. Unfortunately, computer models that combine both aspects of single-population extinction and genetic considerations discussed above with considerations of metapopulation theory are not yet available for developing conservation management strategies.

Nevertheless, managers should be cognizant of the complexities of metapopulation systems. In general, populations distributed over several patches are more secure over the long term than one population located at a single site. This is particularly true if there is gene flow between patches (either natural or through management intervention) and the patches are not susceptible to the same catastrophic threats. In many cases, a captive population can serve as a secure patch that can be used as a source to recolonize other patches through reintroduction efforts and as a reservoir for genetic diversity.

VORTEX

A Stochastic Simulation of the Extinction Process

Version 7

Chapter 3:

Putting PVA to Work in Conservation

Putting Population Viability Analysis to work in endangered species recovery and small population management[1]

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Population Viability Analysis (PVA) is the estimation of extinction probabilities by analyses that incorporate identifiable threats to population survival into models of the extinction process (Brussard 1985; Gilpin and Soulé 1986; Burgman et al. 1993; Lacy 1993a). H. Resit Akçakaya provided an overview of simulation modeling and PVA. I would like now to continue that discussion, providing some of my perspective on PVA, with particular emphasis on the application of PVA to population management. I will draw upon my experiences with wildlife agencies, in order to provide some examples of how PVA can help—and in some cases how it might hinder—species management. At the outset, I need to admit two things about the examples I will relate: (1) the workshops, research efforts, data and certainly the management plans that I will describe result from collaborative efforts by many people. Often, my role was rather minor. I served primarily as a facilitator, or sometimes as a statistician, for the wildlife biologists who did most of the work, and who had the responsibility for managing the species. (2) I will be very selective in my description of lessons that I learned from some of the PVAs in which I have participated. While I might describe just one aspect, positive or negative, about an endangered species program, all conservation and management programs are exceedingly complex, all have strengths and weaknesses, and all benefit from the dedicated efforts of a number of biologists.

The Extinction Process

The primary causes of the decline of many species are obvious and deterministic: populations are over-harvested; natural habitat is converted and lost to the species, often involving the replacement of diverse ecological communities with monocultures; environments are polluted, with the dumping of toxins into the air, water, and soil; local and now even global climates are modified by the actions of humans; and numerous exotic competitors, predators, parasites and diseases are introduced in communities that have never evolved defenses to the new invaders. The primary causes of species decline are usually easy to understand, and often easy to study and model, but usually, though not always, difficult to reverse. Yet the final extinction of most populations often occurs not so much because of a continuation of the pressures that led to the initial decline, but because of bad luck. Chance or stochastic processes usually have little impact on long-term population dynamics, as long as the population is abundant and spread over a wide

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geographic range and a number of habitats. Deterministic processes, such as those listed above, predominate in widespread, still common species, while local chance events impacting subsets of the population will average out across the broader, diverse range. When a population becomes small, isolated, and localized, however, chance events can become important, even dominating the long-term dynamics and fate of a population.

If there exist many small populations that occasionally reinforce each other by exchanging migrants, then the metapopulation can be quite stable even if the component subpopulations are unstable and subject to local extinctions and recolonizations. If the local populations are isolated and independent, however, then over time local extinctions accumulate and eventually result in metapopulation extinction (Ebenhard 1991; Hanski and Gilpin 1991). Unfortunately, the decline of a metapopulation due to the loss of its component subpopulations can be quite steady, thereby masking the underlying stochastic nature of the subpopulation extinctions. Moreover, often we do not respond effectively to the gradual decline of a species over a broad area until the species has been reduced to one or just a few remnant, possibly irretrievably unstable, local populations. Also, migration among unstable subpopulations does not always rescue the metapopulation. In some cases, migration among local population can further destabilize the system (Lindenmayer and Lacy 1994a, 1994b, 1994c).

Many stages in the life history of an organism, and the processes that define the history of a biological population, are essentially stochastic sampling phenomena. Births, deaths, dispersal, disease, sex determination, and transmission of genes between generations all are largely probabilistic phenomena. Small samples intrinsically have greater variance around the probabilistic mean or expectation than do large samples, and therefore small populations will experience greater fluctuations in births, deaths, sex ratio, and genetic variation than will larger populations. The fundamental problem facing small populations is that the fluctuations they experience due to the multiple stages of sampling each generation make it increasingly likely that the populations will, unpredictably, decline to zero. Once populations are small, the probability that they will become extinct can become more strongly determined by the amount of fluctuations in population size than in the mean, deterministic population growth rate. Thus, extinction can be viewed as a process in which once common and widespread populations become reduced to small, isolated fragments due to extrinsic factors, the small remnant populations occasionally and unpredictably go extinct, and the cumulative result of local extinctions is the eventual extinction of the taxon over much or all of its original range (Gilpin and Soulé 1986; Clark et al. 1990).

Shaffer (1981) provided a useful categorization of the stochastic processes that destabilize and threaten small populations into four levels of uncertainty: demographic stochasticity, environmental variation, catastrophic events, and genetic drift. Demographic stochasticity is the random fluctuation in the observed birth rate, death rate, and sex ratio of a population that occur even if the probabilities of birth and death remain constant. Demographic stochasticity would follow binomial distributions and will be important to population viability only in populations that are smaller than a few tens of animals (Goodman 1987), in which the frequency of birth and death events and the sex ratio can deviate far from the statistical expectations. Environmental variation is the fluctuation in the probabilities of birth and death that results from fluctuations in the environment. Weather, the prevalence of enzootic disease, the abundances of prey and predators, and the availability of nest sites or other required microhabitats can all vary, randomly or cyclically, over time. Catastrophic variation is the extreme of environmental variation, but for both methodological and conceptual reasons rare catastrophic events are analyzed separately from the more typical annual or seasonal fluctuations. Catastrophes such as epidemic disease, hurricanes, large-scale fires, and floods are outliers in the distributions of environmental variation. As a result, they have quantitatively and sometimes qualitatively different impacts on wildlife populations (Ewens et al. 1987). Such events are often the cause of the final decline of wildlife populations to extinction (Simberloff 1986, 1988).

Genetic drift is the cumulative and non-adaptive fluctuations in allele frequencies resulting from the random sampling of genes in each generation. This can impede the recovery or accelerate the decline of wildlife populations for several reasons (Lacy 1993b). Inbreeding, not strictly a component of genetic drift but correlated with it in small populations, has been documented to cause loss of fitness in a wide variety of species, including virtually all sexually reproducing animal in which the effects of inbreeding have been carefully studied (Wright 1977; Falconer 1989; O'Brien and Evermann 1988; Ralls et al. 1988; Lacy et al. 1993a). Evidence of loss of fitness includes decreased survival and fecundity and increased susceptibility to disease and other environmental stresses. Even if the immediate loss of fitness of inbred individuals is not large, the loss of genetic variation throughout a population that results from genetic drift will reduce the ability of the population to adapt to future changes in the environment.

Thus, the effects of genetic drift and consequent losses of genetic variation in individuals (e.g., inbreeding) and populations negatively impact demographic rates and increase susceptibility to environmental perturbations and catastrophes. Reduced population growth and greater fluctuations in numbers in turn accelerates genetic drift (Crow and Kimura 1970). These synergistic destabilizing effects of stochastic processes on small populations of wildlife have been described as an "extinction vortex" (Gilpin and Soulé 1986). The size below which a population is likely to be drawn into an extinction vortex can be considered a "minimum viable population" (MVP), although Shaffer (1981) first defined a MVP more stringently as a population that has a 99% probability of persistence for 1000 years. The estimation of MVPs or, more generally, the investigation of the probability of extinction of a population constitutes Population Viability Analysis (Gilpin and Soulé 1986; Gilpin 1989; Shaffer 1990; Boyce 1992).

Managing with PVA

As an approach for examining the extinction process, PVA must consider both deterministic and stochastic factors. The study and management of the deterministic factors is now new: that is what most of the field of wildlife biology is all about. Because the deterministic factors have been studied for decades, most of the emphasis of PVA has been on new techniques that allow us to incorporate also the stochastic factors into assessments and management planning. Therefore, PVAs have tended to accept the deterministic component almost as givens, and then to focus on assessing, predicting, and managing the random, unpredictable, stochastic factors. While it may seem a bit paradoxical to discuss the prediction and management of inherently unpredictable forces, tools and strategies are evolving that can help the wildlife manager to deal with such processes. The application of PVA to the conservation of small, isolated populations is fundamentally an exercise in risk management (Clark et al. 1990; Burgman et al. 1993). Because of the important role of stochastic factors on small populations, it will not be sufficient to stop the deterministic decline of a population. Managers will have to minimize the natural stochasticity of the system, and then put the population into a strong deterministic **increase**, so that it can overcome the stochastic processes and recover to healthy and stable levels.

Because the forces driving population dynamics change as a population becomes small, the tools needed to understand and manage small populations are different from those needed to study and manage large populations, such as of game animals. In a highly stochastic world, we cannot predict the fate of individual animals, nor even of individual populations, but we can determine the probability that a population will follow a given course. This shift from deterministic specification of population performance to description of probability distributions of possible fates is perhaps one of the more difficult concepts for some population managers to incorporate fully into their thinking. It is perhaps even more difficult for policy makers and administrative bureaucracies to deal with probabilistic, uncertain processes.

Much of wildlife management still relies on the assessment of population trends, threats, and management strategies by the few experts who have most intimate field knowledge of the population. While local experts often have a wealth of experience to draw upon, and therefore can provide skilled guidance for conservation programs, such an approach has proven inadequate for reversing the decline of most endangered populations. Humans can assimilate and integrate simultaneously at most a few interacting factors driving a complex process. Therefore, the mental (intuitive) conceptions or models used by experts will incorporate only a subset of the knowledge those experts have gained through years of field research. Most humans also have difficulty accurately assessing probabilistic phenomena, especially when the joint probabilities of many individually rare events must be considered. Finally, even if the mental models of one or a few local experts are comprehensive and accurate, the absence of written specification of the model, its assumptions, and the data applied to the model make intuitive judgements untestable, and therefore inaccessible to challenge or improvement by others as new data and different concepts become available to apply to the problem.

There are three approaches that might be pursued in a PVA. The best approach, or at least the one that provides the most easily defended quantification of the probability of extinction, is to gather empirical data on the frequency with which small, isolated populations of a given species, under specified conditions, go extinct. If the frequency, time course, and causes of extinction can be known from empirical or historical studies, then the wildlife manager can tailor management plans to avoid similar extinctions of remaining populations that are targeted for conservation. For example, Berger (1990) found that isolated populations of bighorn sheep in the Rocky Mountains almost always went extinct within 100 years when the population sizes were below 100 animals. Populations of more than 100 sheep always persisted. The limitations of such empirical determinations of minimum viable populations as a guide for conservation are obvious. If historical data are lacking, such studies would require tens of years (at least) of monitoring tens to hundreds of populations of varying size. Most endangered species would be extinct before such studies could be completed, and often multiple populations for study no longer exist.

At the opposite extreme from empirical studies focused on specific populations are theoretical models that make general predictions about the probabilities of extinction from basic characteristics of taxa, environments, and distributions (Starfield and Bleloch 1986). For example, Goodman (1987) has presented such a model for estimating time to extinction for a few demographic parameters, and theoretical models exist that allow prediction of the rate of loss of genetic variation in isolated populations (Lande and Barrowclough 1987). Unfortunately, such theoretical models are still extremely simple, incorporating only a few of the many stochastic factors that threaten populations. Therefore, such theoretical models may considerably underestimate the overall threat of extinction. Moreover, the dynamics of populations may be driven more by the *interactions* among factors than by the isolated processes. Models that consider threatening processes in isolation may provide misleading representations of population dynamics and lead to ineffective or even counter-productive prescriptions for management (Lacy and Lindenmayer 1994; Lindenmayer and Lacy 1994a, 1994b, 1994c.)

Lacking empirical data on most species of concern, and lacking sufficiently comprehensive theoretical models of extinction, PVA often relies on computer simulation models of population dynamics. Simulation models can be made quite complex, incorporating virtually all of what we know or suspect about the forces controlling the system. In fact, the power of simulation models to simultaneously incorporate a multitude of factors can be one of their limitations (Starfield and Bleloch 1986). Often, so many factors are modeled in an attempt to reproduce reality that the causal factors primarily responsible for driving overall trends cannot be discerned. It is important to balance simplicity of models, so that we can understand the effects of controlling variables, with complexity and completeness, in order to consider all those interacting forces that might be important in the natural system.

The PVAs described below all used the VORTEX computer model (Lacy 1993a). VORTEX is an individual-based simulation that models demographic events (mate selection, birth, sex determination, and death), environmental variation in the probabilities of these events, short-term catastrophic declines in survival or reproduction, and the genetic variation present within and among individuals. Feedback between genetic and demographic processes can be modeled by incorporating inbreeding depression. Linear trends in habitat availability can be modeled, and habitat limitations are simulated by a ceiling model in which additional mortality is imposed across all age classes when the population exceeds the habitat carrying capacity. Multiple populations exchanging migrants, and harvest and supplementation of populations can also be modeled with VORTEX. The VORTEX program, a manual describing its use (Lacy et al. 1993b), and reports from most of the PVA workshops described below are available at minimal cost from the IUCN/SSC Conservation Breeding Specialist Group, 12101 Johnny Cake Ridge Road, Apple Valley, MN 55124, USA.

The Process of Population Viability Analysis

PVA is a process, or a framework for working, and it is often interwoven with several other techniques for managing complex systems. In particular, most of the PVAs with which I have been involved arose from workshops, such as this one focused on conserving the biodiversity of the Fundy ecosystem, convened to address the problems of one or a few species or populations.

The PVA process contains a number of critical components. First, it is essential to gather the experts who have knowledge of the species or problem. Much of science is done by people working independently, often in competition, to achieve their goals. Unfortunately, this tradition has been common in wildlife management and conservation as well. To solve the urgent and difficult problems of conservation, all available knowledge is needed. PVA is certainly not required to bring together experts, but it often facilitates such sharing of expertise because the collective expertise of many is essential for a useful PVA to be completed. For example, the Puerto Rican Parrot PVA workshop (Lacy et al. 1989) brought together individuals who had been studying and managing the remnant population of parrots during sequential, but non-overlapping, periods of time during the past few decades. As just one example of the benefit that comes from such facilitated communication around a conference table, the current management team learned at the workshop from a past team the location of one of the few nest sites of the species. (Unfortunately, a visit to the site revealed that it had been abandoned at some time during the lapse of observation.)

A PVA also requires and therefore facilitates the involvement of a number of agencies and otherwise concerned organizations. For example, the PVA on the two endemic primates of the Tana River Primate Reserve in Kenya (Seal et al. 1991) was convened by the Kenya Wildlife Service, facilitated by the SSC Captive Breeding Specialist Group of the IUCN, benefitted from the expertise contributed by members of the IUCN/SSC Primate Specialist Group, and was sponsored by the World Bank. The involvement of many agencies and interested parties is critical to endangered species recovery. All individuals and agencies have their own needs, goals, mandates, and agendas, and are likely to be most comfortable working with those techniques and approaches with which they are most familiar. Species are not the property of any individual or agency, however, so data, good ideas, and investment in conservation programs are not and should not be owned exclusively by any individual or agency. Personal, organizational, and agency conflicts and inertia can quite effectively block needed conservation (e.g., black-footed ferret: Clark 1989; Florida panther: Alvarez 1993).

An early requirement of a PVA workshop is to determine the conservation problem to be addressed, and to state the goals of the management plan. For example, a workshop focused on the lion tamarins in Brazil (Seal et al. 1990) first proposed a conservation goal of the recovery of the four taxa of lion tamarins to numbers and distributions that would ensure their existence even in the absence of continued interventive management. The PVA, however, revealed that such a goal was unattainable given the limitations of remaining or recoverable habitat. While this outcome was unfortunate, it led to the important recognition that survival of the lion tamarins would probably require interventive management until such time as major habitat reconstruction could be accomplished. Many endangered species programs have not addressed the goal to which they are aspiring. For example, at a PVA and Conservation Assessment and Management Plan workshop on the bird fauna of the Hawaiian Islands (Ellis et al. 1992a, 1992b) it became apparent that the agencies responsible for the conservation of Hawaii's bird fauna had not determined whether their goal was to prevent species extinctions, prevent taxa (species or subspecies) from becoming extinct on any of the islands they presently inhabit, preserve species in sufficient numbers and distribution to allow them to continue to fill ecological roles in the biological communities, or the restoration of taxa to most or all parts of their original ranges. The management actions required to achieve these various levels of conservation are quite different.

PVA requires the assembly of all available data. Often, important information is found in the field notes of researchers or managers, in the heads of those who have worked with and thought about the problems of the species, and in unpublished agency reports, as well as in the published scientific literature. The PVA process can induce the collection of data in anticipation of analysis at a workshop. For example, a Sumatran tiger PVA (IUCN/SSC Captive Breeding Specialist Group, unpublished) helped trigger the systematic collection of data on sightings and signs of tigers in protected areas throughout the island of Sumatra, and collation and integration with a Geographic Information System (GIS) map of habitats and human pressures on those habitats. A PVA for Key deer (Seal and Lacy 1990) revealed a lack of recent data on the population, and consequently an inability to make useful predictions about population viability or optimal management actions. The primary outcome of the PVA process was to recommend research to collect pertinent data on census numbers and factors controlling those numbers.

For some threatened taxa, considerable data exist but the data have been insufficiently analyzed until a PVA is conducted. For example, although most Florida panthers had been monitored regularly by radio-tracking for more than a decade, and almost all deaths and causes of death had been recorded, field biologists had not calculated the mortality rate for the population until asked to do so at a PVA workshop (Seal and Lacy 1989). The field biologists had been concentrating on collecting data, with an eventual goal of publishing results, but they had never been asked to provide the data analyses that should have been underlying management decisions. In the absence of a framework for utilizing information, it is unlikely that data will be analyzed and the implications assessed. When the average annual mortality of Florida panthers was revealed (27% calculated from data available at the time of the PVA workshop; 21% when data from 3 subsequent years were added: Seal and Lacy 1992), response of some at the workshop could be characterized as disbelief—such high mortality, it was said, could not exist without driving the population to extinction. The reality is that mortality was unacceptably high (and outpacing births), and the population was consequently declining toward extinction, even while being the focus of intensive research and monitoring. A result of the PVA and ensuing discussions was that much more aggressive management actions (including captive breeding, translocation to other habitats, and genetic and demographic supplementation with pumas of other subspecies) were recommended (Seal and Lacy 1992).

It is important to specify the assumptions that underlay a PVA, and any consequent management recommendations. The Recovery Plan for the Key deer (U.S. Fish and Wildlife Service 1985) specified an assumption that constrained management options: "Key deer are the product of unique selective forces, mainly a restrictive, insular environment with no natural predators. The management of the Key deer should primarily involve retention of those natural selection factors that influenced their evolution." This position proscribes various interventive management options that might be needed to prevent extinction of the subspecies (e.g., "Population augmentation from a captive herd would never be a substitute for natural reproduction in the Key deer's historic range"). It was important that such limitations were recognized and reiterated before the PVA proceeded. While philosophical and ethical considerations often drive or constrain conservation action (indeed, part of the justification for conservation of biodiversity and healthy ecosystems derives from philosophical stands), unstated or unexamined philosophical positions are often applied inconsistently. In the case of the Key deer, much of the population that is to be managed forever exposed to original natural selection forces in a natural ecosystem feeds daily in the backyard of a woman who places out bags of grain for them, and the primary cause of mortality is road kills. A second assumption of the biologists responsible for the recovery of the population was that the highly skewed sex ratio (about 66% of births are male) was due to an intrinsic population regulatory mechanism that had evolved to prevent over-exploitation of the limited island habitat. This explanation had gone unchallenged until the PVA workshop. At the workshop, evolutionary biologists brought to the discussion pointed out that the theories that were being used to explain self-regulation of populations (group selection acting on a panmictic population) had been discredited about two decades earlier.

The Hawaiian bird conservation planning is constrained by a perspective that no birds bred outside of the islands (in captive breeding facilities) should ever be brought back to the islands for release. While this position derives from a concern for disease transmission (much of the decline of Hawaii's native birds is thought to be due to introduced avian diseases) as much as from any political or philosophical stand, any justification for the restriction must be questioned in light of the fact that wildlife agencies import and release, without quarantine, thousands of exotic gamebirds onto the islands annually.

Once experts are assembled, problems stated and goals set, data gathered and assessed, and assumptions specified, then the PVA process can proceed with what might be considered to be PVA in the narrow or strict sense: estimation of the viability of the population. The available data are used to estimate the parameters that are needed for the model of population dynamics to be applied. Often, data are not available from which to estimate certain key parameters. In those cases, subjective and objective, but non-qualified, information might be solicited from the assembled experts, values might be obtained from data on related species, or a factor might simply be omitted from the model. While such a non-precise process might be very similar to the process of intuitive judgements made by experts, it is important to specify how the parameters for the model were obtained. The resulting limitations of the analyses should acknowledged, and a decision made if, how, by whom, and when the missing data would be collected so that more refined analyses could be conducted. With the PVA model, projections of the most likely fate, and distribution of possible fates, of the population under the specified assumptions are made. Most commonly, the probability of persistence of a population over various time spans is of primary concern. Other output that might be of value include: rates of population growth and fluctuations in growth, projected population sizes, sustainable rates of harvest, rates of loss of genetic variation, and extinction-recolonization dynamics of local populations.

With the projections from the model, the conservation status (degree of threat) of a population and the primary threatening processes or risks can be assessed. For example, PVA of the eastern barred bandicoot in Victoria, Australia (Lacy and Clark 1990) revealed a high probability of extinction of the population within 10-20 years, due to the very high mortality from introduced predators (foxes and feral cats) and road kills. Although simple extrapolation from recent census estimates could have yielded the same dire predictions, the PVA modeling helped to highlight the urgency of more effective conservation action and helped to point to the primary causes of continued decline.

Analysis of whooping cranes (Mirande et al. 1991) revealed a more reassuring result: the population had recovered sufficiently, from a low of 18 birds in 1938 to 146 birds in 1990, that it was no longer in imminent danger of extinction due to demographic stochasticity, environmental variation of the magnitude observed in recent years, or genetic problems. Like any single, small population, the whooping cranes continue to be vulnerable to catastrophes. All breeding occurs within Wood Buffalo National Park in Alberta, Canada, and all the breeding population overwinters along the Texas coast. A disease epidemic in Wood Buffalo, or a storm or oil spill in Texas, could exterminate the population that had been so carefully nurtured away from the brink of extinction.

A similar assessment was made for the Puerto Rican parrot, which had increased from about 16 birds in the early 1970's to 34 wild and 54 captive birds in 1989 (Lacy et al. 1989). Intensive management and protection had pulled the population away from demographic crisis, but it remained vulnerable to catastrophes so long as there was just one localized wild population and the entire captive population was kept in outdoor pens at a breeding facility adjacent to the habitat of the wild flock. In particular, at the PVA workshop it was recognized that severe hurricanes, capable of killing about half of the birds in an area, strike Puerto Rico on average once every 30 years. A localized population is much more vulnerable to such a storm than is a widespread one, and the parrot population was still sufficiently small that a loss of half the population could put it back in jeopardy from demographic and genetic stochasticity. Hurricanes hitting any given locality are not common, but a 1 in 30 annual chance of population decimation was not considered safe. At the PVA workshop, a number of recommendations were made to safeguard the population in the eventuality that such a storm hit the island. Several months later, hurricane Hugo devastated the habitat and killed half of the wild parrots directly or indirectly (e.g., due to predation by hawks of parrots scattered through denuded forest). Some of the workshop recommendations had been implemented by the time the hurricane struck (for example, caging and food supplies were sufficient to protect all of the captive birds in a concrete building), but others were not (no birds had yet been moved to another aviary distant from the primary breeding site).

PVA of the Aruba Island rattlesnake (Odum et al. 1993) revealed the special vulnerability of that species to high juvenile mortality. Education programs on the island now focus on encouraging people to take pride in their native rattlesnake and protect, not kill, the snakes.

Because so much of a PVA—the data, the model, and even the interpretation of output—is uncertain, an essential component of the PVA process is sensitivity testing. Ranges of plausible values for uncertain parameters should be tested, to determine what effects those uncertainties might have on the results. In addition, several different PVA models might be examined, or the same general model tested under different structural assumptions. Different participants in the process should assess and interpret the results. Such sensitivity testing reveals which components of the data, model, and interpretation have the largest impact on the population projections. This will highlight which aspects of the biology of the population and its situation contribute most to its vulnerability and, therefore, which aspects might be most effectively targeted for management. In addition, uncertain parameters that have a strong impact on results are those which might be the focus of future research efforts, to better specify the dynamics of the population. Close monitoring of such parameters might also be important for testing the assumptions behind the selected management options and for assessing the success of conservation efforts.

Closely parallel to the testing of uncertainties in the present situation is the testing of options for management. In many conservation and management programs, courses of action are outlined, but expected outcomes of the actions are not specified. PVA modeling allows one to test the expected results of any given management action, under the assumptions of the model and within the limitations of present knowledge, on the computer before implementation in the field. This process can guide selection of the management options most likely, given current knowledge, to be effective, and will define target recovery goals that should be obtained if our knowledge is adequate and the recommended actions are followed. In the case of the eastern barred bandicoot, exploration of the efficacy of options suggested that only if **all** of the options being considered (reduced speed limits to reduce road kills, feral cat control, and planting of strips of vegetation for protective cover) were implemented quickly would there be a good probability that the population could be rescued from its decline toward extinction (Maguire et al. 1990). None of these were fully implemented, and the wild population is probably now extinct. A captive population is secure, however, and is being used to reestablish bandicoots in more secure natural areas and semi-natural enclosures. PVA of the black rhinoceros in Kenya's 11 rhino sanctuaries (Foose et al. 1993) suggested that periodic movement of rhinos between fenced sanctuaries to reduce inbreeding and demographic fluctuations would be necessary to stabilize the populations in the smaller parks. Moreover, the modeling provided estimates of the rate at which the larger populations would be able to provide surplus animals for translocation.

The Kenya black rhino workshop provides a good example of some other factors common to many PVAs, and of how PVAs can assist wildlife managers who adopt it as one of the tools of their trade. Because probabilistic phenomena will necessarily fluctuate in small populations across years, even if the underlying causes are constant, it is difficult to discern or project long-term trends from short-term data. Moreover, there is an understandable tendency for researchers and managers to focus on recent events, especially when assessments are based primarily on subjective integration of field observations rather than on quantitative analysis of all the data available. It had been observed that the rhino populations in several of the sanctuaries in Kenya had not increased for several years, while others were showing good reproduction. The first, intuitive assessment was that the habitat quality may be deficient in some way in those areas not showing good reproduction. Fortunately, there are very good data on the Kenya rhino populations since 1985. Analysis of these data revealed the same inter-calf interval in each of the sanctuaries, when averaged over the past decade. With a 4-year inter-calf interval, short-term fluctuations in the reproductive output of populations that had a small number of breeding age females was, in retrospect, not surprising. Consideration of the variation in population growth expected in stochastic systems also helped ameliorate another worry of the wildlife managers in Kenya. It has been suggested that healthy rhino populations would increase at a rate of about 12% per annum. While such a rate is possible over the short term, analysis of the life table (potential birth and death rates) revealed that even under good conditions, black rhinos should not be expected to sustain such growth. The long inter-calf interval necessitated by prolonged maternal care followed by long gestation, coupled with even low natural mortality, cannot yield a sustained growth rate as high as had been presumed. The 5% annual growth observed in the Kenya rhino populations was almost as much as could be sustained given low mortality and good breeding success.

The use of the PVA process to help guide conservation decisions is not a singular event, in which an analysis can be completed, management actions recommended and implemented, and conservation thereby assured. The many uncertainties in the process mandate that PVA be used as a tool in an adaptive management framework. In adaptive management, the lack of knowledge adequate to predict with certainty in best course of action is recognized, management actions are designed in such a way that monitoring will allow testing of the adequacy of our model and understanding, and corrective adjustments to management plans are made whenever the accumulating data suggest that the present course is inadequate to achieve the goals and a better strategy exists (Holling 1978). The urgency of the biodiversity crisis will not permit us ethically to refrain from aggressive conservation action until we have scientifically sound understanding of all the factors that drive population, community, and ecosystem dynamics. PVA provides a powerful tool for making use of the information we do have, in a well-documented process that is open to challenge and improvement. PVA can, therefore, make it easier for wildlife managers to succeed in the very difficult and important job of safeguarding the future of wildlife populations.

Limitations of PVA

In spite of the rapid development of PVA in the past decade, we are still in the early days of PVA, and the learning curve is steep. Population Viability Analysis, as practiced today, has many limitations, is quite vulnerable to criticism on a number of fronts, and can be abused intentionally or unintentionally almost as easily as it can be put to the service of conservation. First, natural systems are extremely complex, we understand too little to accurately predict population dynamics in nature, and even the most comprehensive models incorporate just a subset of what we do know about population biology. In particular, there are likely a multitude of interactions among factors that can impact populations in ways not commonly modeled. For example, increasing fragmentation of habitats not only reduces population sizes, and isolates populations from potential sources of migrants, but also probably increases mortality of migrants seeking available habitat, and may change dispersal patterns altogether. At a higher level of complexity, changes in the abundance and distribution of one species in a biological community have effects on many others, which may in turn feed back, positively or negatively, on the focal species. It is easy to model the density dependence in survival and reproduction that arise from interactions among individuals within a species; it is quite another matter to contemplate the density dependent feedbacks that come about indirectly through relationships with other components of the community.

In many ways, our understanding of the extinction process is inadequate. For example, although inbreeding is known to depress a variety of aspects of fitness in many species, the variation among species in the severity of inbreeding depression is very poorly understood (Lacy 1992). The underlying genetic causes of inbreeding depression have not been confirmed (Charlesworth and Charlesworth 1987) and, as a consequence, it is not known to what extent natural populations could become purged of deleterious genes and adapted to inbreeding (Lacy 1992). Moreover, almost all data on inbreeding are derived, understandably, from laboratory populations or domesticated livestock or crop plants. It is now known how much more severe the impacts of inbreeding might be in natural populations that encounter many stresses from captive populations are sheltered (Lacy et al. 1993a; Lacy 1993b).

To date, most (maybe all) of the PVA models available assume that population changes occur at discrete time steps. Many species reproduce seasonally, but many do not and few have strictly seasonal die-off. Discrete-time models are probably fully adequate as approximations of many continuous time systems, but the difference between the behavior of discrete-time vs. continuous-time PVA models has yet to be explored.

Just as the temporal structure of population dynamics is simplified in PVA, so the spatial structure is modeled as an unrealistically simple system. Existing models incorporate minimal consideration of the spatial structure of habitats, and of individuals within those habitats. Such variation among habitats and among individuals could lead to much greater stochastic variation in demographic processes, and in the breeding systems that determine patterns of genetic variation. Alternatively, such variation could help buffer populations from perturbations by minimizing the likelihood that all habitats and individuals would be impacted simultaneously and equally by a stress.

For very few species are there long-term data that allow estimation of the amplitude of environmental fluctuations. We have even poorer data on the frequency and impacts of catastrophes such as epidemic disease and severe weather. Increasingly, shifts in human populations and their use of the environment also constitute catastrophic and poorly predicted impacts on natural populations.

There is a need for validation of PVA models. Few of the computer models have received sufficient testing to be reasonably confident that they are free of programming errors that would seriously affect population projections. Different programs that are thought to model the same processes in similar ways ought to be applied to common data sets to determine if they yield similar results. Even if the computer programming is free of bugs, there remains a need for experimental testing of the extent to which the simple models we build can predict the aspects of the natural population dynamics that are of concern. Tests could consist of examination of historical data, or experimental populations could be monitored to determine if living models perform similarly to computer models of natural populations. The long-term data on whooping cranes (for which counts of birds arriving at the wintering grounds have been made every year since 1938, and counts of chicks made at the breeding grounds every year since 1969) allowed one test of the VORTEX model applied in the PVA. The model generated a mean and, more importantly, variance in population growth comparable to that observed in nature (Mirande et al. 1991).

It is regrettably easy to misuse PVAs. Often those using a PVA model have a poor understanding of the assumptions, algorithms, and structure of the model they are using. Also, the programmer rarely had knowledge of the specifics of the biology of the situation being modeled. There is a risk that use of a PVA simulation model can be an exercise in the data-blind (the programmer, through the program) leading the algorithm-blind (the field biologist or other user of the program). Close collaboration, or very good documentation, might be necessary to avoid such a predicament.

PVA allows the testing of impacts of factors in isolation or in combinations. It therefore facilitates the separation of spurious correlations from causal factors. Unless a lot of sensitivity testing is done, however, it is easy to come to incorrect conclusions about which of the numerous factors in a PVA model are primary determinants of population dynamics. Another easy error to make in using PVA is to assume that the model incorporates everything of interest. A PVA simulation program can only include those processes that are known to the programmer, which is likely to be a subset of what might be known to the field biologists which in turn will definitely be a subset of those processes that impact natural populations. Because PVAs consider only those threatening processes for which we have knowledge, for which we can develop algorithms for modeling, and for which we have some data, it is likely that PVAs will underestimate the vulnerability of most populations to extinction. We cannot know the extent by which analyses underestimate threats, but wildlife managers will need to determine how large a margin for error to build into management plans.

Although several good, general PVA simulation models are available and are being used on a wide variety of species, no general model would be as good as a comparable model designed specifically for the population of concern, and designed by (or at least in collaboration with) the biologists who will be applying the model (Starfield and Bleloch 1986). There are risks in developing models specific to a given situation, however. The general models available have gone through extensive testing. Serious conceptual and programming errors might remain, but they are far less likely than in a model developed for and tested on only one population. In addition, through use of the general models by many biologists, the models have evolved considerably. It would be difficult for one or a few biologists to conceive of the range of factors and issues that have been contributed by many users to the development of the widely used models.

Most PVA models to date were developed to model populations of vertebrates that are long-lived with low fecundity (typically mammals, birds, and reptiles). The life histories, primary sources of stochasticity, threats to persistence, and even how an individual is defined are often very different for fish, invertebrates, and plants. VORTEX has, with modification, been applied to an invertebrate with a simple life history (Karner blue butterfly: Seal et al. 1993), and Menges (1990) developed a PVA model for a plant. There is a need for further exploration of the PVA approaches with fish, highly fecund amphibians, invertebrates, and plants.

PVA is, by definition, an assessment of the probability of persistence of a population over defined time frames. Yet, persistence of a population, while a necessary condition for effective conservation of natural systems, is often not sufficient. Prevention of extinction is the last stand for conservationists, but the goals should be higher: conservation of functional biological communities and ecosystems. PVA usually ignores the functional role of a species in a community. A species, such as the American bison, can be functionally extinct in terms of no longer filling its original role in nature, even as it is touted as a conservation success story and would, by PVA, be considered safe from extinction and viable. Perhaps the approach of PVA could be the first step to producing Community Viability Analysis (CVA) or Ecosystem Viability Analysis (EVA).

PVA has been expanded in other dimensions recently. The IUCN/SSC Conservation Breeding Specialist Group (CBSG) now uses the term Population **and Habitat** Viability Assessment (PHVA) to highlight a growing emphasis on incorporating considerations of habitat changes when modeling the viability of populations. CBSG has also begun to explore incorporating analyses of human populations and their patterns of resource use in the PVA framework (e.g., Indian rhino PHVA: Walker and Molur 1994).

Strengths of PVA

Most of the limitations of PVA discussed above are also limitations, often to a greater extent, of the more traditional population ecology methodologies, such as life table analysis. PVA has added dimensions to the study, management, and conservation of wildlife not well considered previously, but it is not a final, all-encompassing solution to the problems of the conservation of biological populations. The strengths that PVA has brought to wildlife conservation have been described by Soulé (1987), Gilpin (1989), Shaffer (1990), Clark et al. (1991), Burgman et al. (1993), and Lindenmayer et al. (1991, 1993). Some of the strengths of the PVA approach are summarized below.

Most fundamentally, PVA is a process for explicitly incorporating what we do know about population dynamics into an overall model that will facilitate examination and testing of various hypotheses about the viability of small populations. PVA modeling allows analysis of the role of stochasticity in population dynamics, using probability theory and simulation to yield probabilistic predictions of fundamentally unpredictable processes. The focus on probabilities, rather than certainties, with a recognition of the impact of rare, stochastic events, is an important advance in wildlife biology. The proper use of PVA forces specification of goals, assumptions, and data—three critical components of wildlife management that are lacking or only implicit in many conservation efforts. PVA can help to identify critical factors for study, management, and monitoring. By making testable predictions about the extinction process, PVA can help bring wildlife population management and parts of conservation biology more solidly within the realm of falsifiable science. It will be interesting to see the extent to which predictions arising from PVAs are tested in conservation practice. For some practitioners, the vulnerability of management plans based on PVA to challenge, reassessment, and falsification might not be welcomed. PVA logically leads to an adaptive management process, in which decisions made on the best available knowledge are used to design programs which are most likely to succeed and which simultaneously provide opportunities to improve knowledge so as to better assure future success.

One of the most common uses of PVA models is as a teaching tool. The exploration of the likely responses and the range of possible responses of a population to changes in various parameters is an ideal way for students and professionals to explore population biology. PVA provides the ability to experiment with a model of a natural system, even exploring effects and parameter spaces not before examined by anyone else. PVA models have already been extremely useful research tools that have expanded our understanding of population dynamics beyond what had been discerned from analytical theory (e.g., Lindenmayer and Lacy 1994a, 1994b, 1994c; Lacy and Lindenmayer 1994).

The Future of PVA

PVA is a powerful tool for studying complex population dynamics, assisting biologists in quantifying, analyzing, projecting, and managing small populations of wildlife. It relies fundamentally on integration with other techniques, and this dependence is helping to foster development of allied areas in conservation biology, and helping to foster collaborative efforts by people working in varied disciplines. Wildlife populations face multiple risks in a world dominated and massively changed by humans. It is essential that we use multiple resources to conserve as much of the rich biota of our shared environment as possible.

PVA has been recommended by an Australian federal commission (Resource Assessment Commission 1992) as one tool that should be applied to ensure that resource management decisions do not jeopardize wildlife populations. The U.S. Fish and Wildlife Service, the Kenya Wildlife Service, and the governments of Indonesia, India, Argentina, and other nations have used PVA to address some of their most difficult species management issues. Canada and Australia have taken the use of PVA one step further by convening workshops to train their agency wildlife biologists in the use of the techniques. Use of outside “experts” alone to practice PVA leaves those charged with implementing conservation plans too far outside of the process for successful application to be likely.

Finally, it has been proposed (Mace and Lande 1991) that listing of taxa as Endangered, Vulnerable, or otherwise threatened with extinction should be based on quantitative definitions of categories of threat, and assignments of species to those categories should, to the extent possible, be based on clearly defined, quantitative criteria. If IUCN and governmental listings of threatened taxa, and legal protection for endangered taxa (such as the Convention on International Trade in Endangered Species, CITES) become based on probabilities of extinction over defined time periods, and associated criteria for abundance, distribution, and trends as indicators of population viability, then PVA will have to become more powerful, more widely applicable, better validated, more widely understood, and much more commonly used. While the challenge in developing the science and getting it applied appropriately is formidable, the alternative is continued reliance on intuition, undocumented and untestable "expert" judgements, single-factor analysis, overly simplistic rules of thumb and "magic numbers", and marketability to the public as the principles guiding the conservation of wildlife populations. The management of wildlife populations as part of a conservation strategy must become a more objective, open, holistic, and testable process.

VORTEX

A Stochastic Simulation of the Extinction Process

Version 7

Chapter 4:

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A Stochastic Simulation of the Extinction Process

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Chapter 5:

VORTEX Technical Reference

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VORTEX: A Computer Simulation Model for Population Viability Analysis

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Abstract

Population Viability Analysis (PVA) is the estimation of extinction probabilities by analyses that incorporate identifiable threats to population survival into models of the extinction process. Extrinsic forces, such as habitat loss, over-harvesting, and competition or predation by introduced species, often lead to population decline. Although the traditional methods of wildlife ecology can reveal such deterministic trends, random fluctuations that increase as populations become smaller can lead to extinction even of populations that have, on average, positive population growth when below carrying capacity. Computer simulation modelling provides a tool for exploring the viability of populations subjected to many complex, interacting deterministic and random processes. One such simulation model, VORTEX, has been used extensively by the Captive Breeding Specialist Group (Species Survival Commission, IUCN), by wildlife agencies, and by university classes. The algorithms, structure, assumptions and applications of VORTEX are described in this paper.

VORTEX models population processes as discrete, sequential events, with probabilistic outcomes. VORTEX simulates birth and death processes and the transmission of genes through the generations by generating random numbers to determine whether each animal lives or dies, to determine the number of progeny produced by each female each year, and to determine which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Fecundity is assumed to be independent of age after an animal reaches reproductive age. Mortality rates are specified for each pre-reproductive age–sex class and for reproductive-age animals. Inbreeding depression is modelled as a decrease in viability in inbred animals.

The user has the option of modelling density dependence in reproductive rates. As a simple model of density dependence in survival, a carrying capacity is imposed by a probabilistic truncation of each age class if the population size exceeds the specified carrying capacity. VORTEX can model linear trends in the carrying capacity. VORTEX models environmental variation by sampling birth rates, death rates, and the carrying capacity from binomial or normal distributions. Catastrophes are modelled as sporadic random events that reduce survival and reproduction for one year. VORTEX also allows the user to supplement or harvest the population, and multiple subpopulations can be tracked, with user-specified migration among the units.

VORTEX outputs summary statistics on population growth rates, the probability of population extinction, the time to extinction, and the mean size and genetic variation in extant populations.

VORTEX necessarily makes many assumptions. The model it incorporates is most applicable to species with low fecundity and long lifespans, such as mammals, birds and reptiles. It integrates the interacting effects of many of the deterministic and stochastic processes that have an impact on the viability of small populations, providing opportunity for more complete analysis than is possible by other techniques. PVA by simulation modelling is an important tool for identifying populations at risk of extinction, determining the urgency of action, and evaluating options for management.

Introduction

Many wildlife populations that were once widespread, numerous, and occupying contiguous habitat, have been reduced to one or more small, isolated populations. The causes of the original decline are often obvious, deterministic forces, such as over-harvesting,

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habitat destruction, and competition or predation from invasive introduced species. Even if the original causes of decline are removed, a small isolated population is vulnerable to additional forces, intrinsic to the dynamics of small populations, which may drive the population to extinction (Shaffer 1981; Soulé 1987; Clark and Seebeck 1990). Of particular impact on small populations are stochastic processes. With the exception of aging, virtually all events in the life of an organism are stochastic. Mating, reproduction, gene transmission between generations, migration, disease and predation can be described by probability distributions, with individual occurrences being sampled from these distributions. Small samples display high variance around the mean, so the fates of small wildlife populations are often determined more by random chance than by the mean birth and death rates that reflect adaptations to their environment.

Although many processes affecting small populations are intrinsically indeterminate, the average long-term fate of a population and the variance around the expectation can be studied with computer simulation models. The use of simulation modelling, often in conjunction with other techniques, to explore the dynamics of small populations has been termed Population Viability Analysis (PVA). PVA has been increasingly used to help guide management of threatened species. The Resource Assessment Commission of Australia (1991) recently recommended that 'estimates of the size of viable populations and the risks of extinction under multiple-use forestry practices be an essential part of conservation planning'. Lindenmayer *et al.* (1993) describe the use of computer modelling for PVA, and discuss the strengths and weaknesses of the approach as a tool for wildlife management.

In this paper, I present the PVA program VORTEX and describe its structure, assumptions and capabilities. VORTEX is perhaps the most widely used PVA simulation program, and there are numerous examples of its application in Australia, the United States of America and elsewhere.

The Dynamics of Small Populations

The stochastic processes that have an impact on populations have been usefully categorised into demographic stochasticity, environmental variation, catastrophic events and genetic drift (Shaffer 1981). Demographic stochasticity is the random fluctuation in the observed birth rate, death rate and sex ratio of a population even if the probabilities of birth and death remain constant. On the assumption that births and deaths and sex determination are stochastic sampling processes, the annual variations in numbers that are born, die, and are of each sex can be specified from statistical theory and would follow binomial distributions. Such demographic stochasticity will be important to population viability only in populations that are smaller than a few tens of animals (Goodman 1987), in which cases the annual frequencies of birth and death events and the sex ratios can deviate far from the means. The distribution of annual adult survival rates observed in the remnant population of whooping cranes (*Grus americana*) (Mirande *et al.* 1993) is shown in Fig. 1. The innermost curve approximates the binomial distribution that describes the demographic stochasticity expected when the probability of survival is 92·7% (mean of 45 non-outlier years).

Environmental variation is the fluctuation in the probabilities of birth and death that results from fluctuations in the environment. Weather, the prevalence of enzootic disease, the abundances of prey and predators, and the availability of nest sites or other required microhabitats can all vary, randomly or cyclically, over time. The second narrowest curve on Fig. 1 shows a normal distribution that statistically fits the observed frequency histogram of crane survival in non-outlier years. The difference between this curve and the narrower distribution describing demographic variation must be accounted for by environmental variation in the probability of adult survival.

Catastrophic variation is the extreme of environmental variation, but for both methodological and conceptual reasons rare catastrophic events are analysed separately from the more typical annual or seasonal fluctuations. Catastrophes such as epidemic disease,

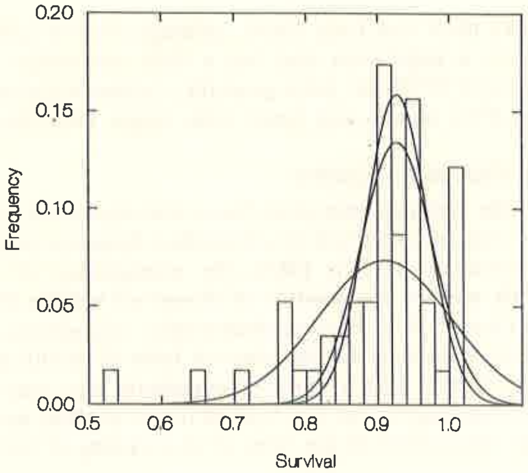

Fig. 1. Frequency histogram of the proportion of whooping cranes surviving each year, 1938–90. The broadest curve is the normal distribution that most closely fits the overall histogram. Statistically, this curve fits the data poorly. The second highest and second broadest curve is the normal distribution that most closely fits the histogram, excluding the five leftmost bars (7 outlier 'catastrophe' years). The narrowest and tallest curve is the normal approximation to the binomial distribution expected from demographic stochasticity. The difference between the tallest and second tallest curves is the variation in annual survival due to environmental variation.

hurricanes, large-scale fires, and floods are outliers in the distribution of environmental variation (e.g. five leftmost bars on Fig. 1). As a result, they have quantitatively and sometimes qualitatively different impacts on wildlife populations. (A forest fire is not just a very hot day.) Such events often precipitate the final decline to extinction (Simberloff 1986, 1988). For example, one of two populations of whooping crane was decimated by a hurricane in 1940 and soon after went extinct (Doughty 1989). The only remaining population of the black-footed ferret (*Mustela nigripes*) was being eliminated by an outbreak of distemper when the last 18 ferrets were captured (Clark 1989).

Genetic drift is the cumulative and non-adaptive fluctuation in allele frequencies resulting from the random sampling of genes in each generation. This can impede the recovery or accelerate the decline of wildlife populations for several reasons (Lacy 1993). Inbreeding, not strictly a component of genetic drift but correlated with it in small populations, has been documented to cause loss of fitness in a wide variety of species, including virtually all sexually reproducing animals in which the effects of inbreeding have been carefully studied (Wright 1977; Falconer 1981; O'Brien and Evermann 1988; Ralls *et al.* 1988; Lacy *et al.* 1993). Even if the immediate loss of fitness of inbred individuals is not large, the loss of genetic variation that results from genetic drift may reduce the ability of a population to adapt to future changes in the environment (Fisher 1958; Robertson 1960; Selander 1983).

Thus, the effects of genetic drift and consequent loss of genetic variation in individuals and populations have a negative impact on demographic rates and increase susceptibility to environmental perturbations and catastrophes. Reduced population growth and greater fluctuations in numbers in turn accelerate genetic drift (Crow and Kimura 1970). These synergistic destabilising effects of stochastic process on small populations of wildlife have been described as an 'extinction vortex' (Gilpin and Soulé 1986). The size below which a population is likely to be drawn into an extinction vortex can be considered a 'minimum viable population' (MVP) (Seal and Lacy 1989), although Shaffer (1981) first defined a MVP more stringently as a population that has a 99% probability of persistence for 1000 years. The estimation of MVPs or, more generally, the investigation of the probability of extinction constitutes PVA (Gilpin and Soulé 1986; Gilpin 1989; Shaffer 1990).

Methods for Analysing Population Viability

An understanding of the multiple, interacting forces that contribute to extinction vortices is a prerequisite for the study of extinction–recolonisation dynamics in natural populations inhabiting patchy environments (Gilpin 1987), the management of small populations (Clark and Seebeck 1990), and the conservation of threatened wildlife (Shaffer 1981, 1990; Soulé 1987; Mace and Lande 1991). Because demographic and genetic processes in small populations are inherently unpredictable, the expected fates of wildlife populations can be described in terms of probability distributions of population size, time to extinction, and genetic variation. These distributions can be obtained in any of three ways: from analytical models, from empirical observation of the fates of populations of varying size, or from simulation models.

As the processes determining the dynamics of populations are multiple and complex, there are few analytical formulae for describing the probability distributions (e.g. Goodman 1987; Lande 1988; Burgmann and Gerard 1990). These models have incorporated only few of the threatening processes. No analytical model exists, for example, to describe the combined effect of demographic stochasticity and loss of genetic variation on the probability of population persistence.

A few studies of wildlife populations have provided empirical data on the relationship between population size and probability of extinction (e.g. Belovsky 1987; Berger 1990; Thomas 1990), but presently only order-of-magnitude estimates can be provided for MVPs of vertebrates (Shaffer 1987). Threatened species are, by their rarity, unavailable and inappropriate for the experimental manipulation of population sizes and long-term monitoring of undisturbed fates that would be necessary for precise empirical measurement of MVPs. Retrospective analyses will be possible in some cases, but the function relating extinction probability to population size will differ among species, localities and times (Lindenmayer *et al.* 1993).

Modelling the Dynamics of Small Populations

Because of the lack of adequate empirical data or theoretical and analytical models to allow prediction of the dynamics of populations of threatened species, various biologists have turned to Monte Carlo computer simulation techniques for PVA. By randomly sampling from defined probability distributions, computer programs can simulate the multiple, interacting events that occur during the lives of organisms and that cumulatively determine the fates of populations. The focus is on detailed and explicit modelling of the forces impinging on a given population, place, and time of interest, rather than on delineation of rules (which may not exist) that apply generally to most wildlife populations. Computer programs available to PVA include SPGPC (Grier 1980*a*, 1980*b*), GAPPS (Harris *et al.* 1986), RAMAS (Ferson and Akçakaya 1989; Akçakaya and Ferson 1990; Ferson 1990), FORPOP (Possingham *et al.* 1991), ALEX (Possingham *et al.* 1992), and SIMPOP (Lacy *et al.* 1989; Lacy and Clark 1990) and its descendant VORTEX.

SIMPOP was developed in 1989 by converting the algorithms of the program SPGPC (written by James W. Grier of North Dakota State University) from BASIC to the C programming language. SIMPOP was used first in a PVA workshop organised by the Species Survival Commission's Captive Breeding Specialist Group (IUCN), the United States Fish and Wildlife Service, and the Puerto Rico Department of Natural Resources to assist in planning and assessing recovery efforts for the Puerto Rican crested toad (*Peltophryne lemur*). SIMPOP was subsequently used in PVA modelling of other species threatened with extinction, undergoing modification with each application to allow incorporation of additional threatening processes. The simulation program was renamed VORTEX (in reference to the extinction vortex) when the capability of modelling genetic processes was implemented in 1989. In 1990, a version allowing modelling of multiple populations was briefly named VORTICES. The only version still supported, with all capabilities of each previous version, is VORTEX Version 5.1.

VORTEX has been used in PVA to help guide conservation and management of many species, including the Puerto Rican parrot (*Amazona vittata*) (Lacy *et al.* 1989), the Javan rhinoceros (*Rhinoceros sondaicus*) (Seal and Foose 1989), the Florida panther (*Felis concolor coryi*) (Seal and Lacy 1989), the eastern barred bandicoot (*Perameles gunnii*) (Lacy and Clark 1990; Maguire *et al.* 1990), the lion tamarins (*Leontopithecus rosalia* ssp.) (Seal *et al.* 1990), the brush-tailed rock-wallaby (*Petrogale penicillata penicillata*) (Hill 1991), the mountain pygmy-possum (*Burramys parvus*), Leadbeater's possum (*Gymnobelideus leadbeateri*), the long-footed potoroo (*Potorous longipes*), the orange-bellied parrot (*Neophema chrysogaster*) and the helmeted honeyeater (*Lichenostomus melanops cassidix*) (Clark *et al.* 1991), the whooping crane (*Grus americana*) (Mirande *et al.* 1993), the Tana River crested mangabey (*Cercocebus galeritus galeritus*) and the Tana River red colobus (*Colobus badius rufomitratus*) (Seal *et al.* 1991), and the black rhinoceros (*Diceros bicornis*) (Foose *et al.* 1992). In some of these PVAs, modelling with VORTEX has made clear the insufficiency of past management plans to secure the future of the species, and alternative strategies were proposed, assessed and implemented. For example, the multiple threats to the Florida panther in its existing habitat were recognised as probably insurmountable, and a captive breeding effort has been initiated for the purpose of securing the gene pool and providing animals for release in areas of former habitat. PVA modelling with VORTEX has often identified a single threat to which a species is particularly vulnerable. The small but growing population of Puerto Rican parrots was assessed to be secure, except for the risk of population decimation by hurricane. Recommendations were made to make available secure shelter for captive parrots and to move some of the birds to a site distant from the wild flock, in order to minimise the damage that could occur in a catastrophic storm. These recommended actions were only partly implemented when, in late 1989, a hurricane killed many of the wild parrots. The remaining population of about 350 Tana River red colobus were determined by PVA to be so fragmented that demographic and genetic processes within the 10 subpopulations destabilised population dynamics. Creation of habitat corridors may be necessary to prevent extinction of the taxon. In some cases, PVA modelling has been reassuring to managers: analysis of black rhinos in Kenya indicated that many of the populations within sanctuaries were recovering steadily. Some could soon be used to provide animals for re-establishment or supplementation of populations previously eliminated by poaching. For some species, available data were insufficient to allow definitive PVA with VORTEX. In such cases, the attempt at PVA modelling has made apparent the need for more data on population trends and processes, thereby helping to justify and guide research efforts.

Description of VORTEX

Overview

The VORTEX computer simulation model is a Monte Carlo simulation of the effects of deterministic forces, as well as demographic, environmental and genetic stochastic events, on wildlife populations. VORTEX models population dynamics as discrete, sequential events that occur according to probabilities that are random variables, following user-specified distributions. The input parameters used by VORTEX are summarised in the first part of the sample output given in the Appendix.

VORTEX simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, reproduction, mortality, increment of age by one year, migration among populations, removals, supplementation, and then truncation (if necessary) to the carrying capacity. The program was designed to model long-lived species with low fecundity, such as mammals, birds and reptiles. Although it could and has been used in modelling highly fecund vertebrates and invertebrates, it is awkward to use in such cases as it requires complete specification of the percentage of females producing each possible clutch size. Moreover, computer memory limitations often hamper such analyses. Although VORTEX iterates life events on an annual cycle, a user could model 'years' that are other than 12 months' duration. The simulation of the population is itself iterated to reveal the distribution of fates that the population might experience.

Demographic Stochasticity

VORTEX models demographic stochasticity by determining the occurrence of probabilistic events such as reproduction, litter size, sex determination and death with a pseudo-random number generator. The probabilities of mortality and reproduction are sex-specific and pre-determined for each age class up to the age of breeding. It is assumed that reproduction and survival probabilities remain constant from the age of first breeding until a specified upper limit to age is reached. Sex ratio at birth is modelled with a user-specified constant probability of an offspring being male. For each life event, if the random value sampled from the uniform 0–1 distribution falls below the probability for that year, the event is deemed to have occurred, thereby simulating a binomial process.

The source code used to generate random numbers uniformly distributed between 0 and 1 was obtained from Maier (1991), according to the algorithm of Kirkpatrick and Stoll (1981). Random deviates from binomial distributions, with mean p and standard deviation s, are obtained by first determining the integral number of binomial trials, N, that would produce the value of s closest to the specified value, according to

$$N = p(1-p)/s^2 \, .$$

N binomial trials are then simulated by sampling from the uniform 0–1 distribution to obtain the desired result, the frequency or proportion of successes. If the value of N determined for a desired binomial distribution is larger than 25, a normal approximation is used in place of the binomial distribution. This normal approximation must be truncated at 0 and at 1 to allow use in defining probabilities, although, with such large values of N, s is small relative to p and the truncation would be invoked only rarely. To avoid introducing bias with this truncation, the normal approximation to the binomial (when used) is truncated symmetrically around the mean. The algorithm for generating random numbers from a unit normal distribution follows Latour (1986).

VORTEX can model monogamous or polygamous mating systems. In a monogamous system, a relative scarcity of breeding males may limit reproduction by females. In polygamous or monogamous models, the user can specify the proportion of the adult males in the breeding pool. Males are randomly reassigned to the breeding pool each year of the simulation, and all males in the breeding pool have an equal chance of siring offspring.

The 'carrying capacity', or the upper limit for population size within a habitat, must be specified by the user. VORTEX imposes the carrying capacity via a probabilistic truncation whenever the population exceeds the carrying capacity. Each animal in the population has an equal probability of being removed by this truncation.

Environmental Variation

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as might result from environmental variation. To model environmental variation, each demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modelled as binomial distributions. Environmental variation in carrying capacity is modelled as a normal distribution. The variance across years in the frequencies of births and deaths resulting from the simulation model (and in real populations) will have two components: the demographic variation resulting from a binomial sampling around the mean for each year, and additional fluctuations due to environmental variation and catastrophes (see Fig. 1 and section on The Dynamics of Small Populations, above).

Data on annual variations in birth and death rates are important in determining the probability of extinction, as they influence population stability (Goodman 1987). Unfortunately, such field information is rarely available (but see Fig. 1). Sensitivity testing, the examination of a range of values when the precise value of a parameter is unknown, can help to identify whether the unknown parameter is important in the dynamics of a population.

Catastrophes

Catastrophes are modelled in VORTEX as random events that occur with specified probabilities. Any number of types of catastrophes can be modelled. A catastrophe will occur if a randomly generated number between zero and one is less than the probability of occurrence. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are multiplied by severity factors. For example, forest fires might occur once in 50 years, on average, killing 25% of animals, and reducing breeding by survivors by 50% for the year. Such a catastrophe would be modelled as a random event with 0·02 probability of occurrence each year, and severity factors of 0·75 for survival and 0·50 for reproduction.

Genetic Processes

Genetic drift is modelled in VORTEX by simulation of the transmission of alleles at a hypothetical locus. At the beginning of the simulation, each animal is assigned two unique alleles. Each offspring is randomly assigned one of the alleles from each parent. Inbreeding depression is modelled as a loss of viability during the first year of inbred animals. The impacts of inbreeding are determined by using one of two models available within VORTEX: a Recessive Lethals model or a Heterosis model.

In the Recessive Lethals model, each founder starts with one unique recessive lethal allele and a unique, dominant non-lethal allele. This model approximates the effect of inbreeding if each individual in the starting population had one recessive lethal allele in its genome. The fact that the simulation program assumes that all the lethal alleles are at the same locus has a very minor impact on the probability that an individual will die because of homozygosity for one of the lethal alleles. In the model, homozygosity for different lethal alleles are mutually exclusive events, whereas in a multilocus model an individual could be homozygous for several lethal alleles simultaneously. By virtue of the death of individuals that are homozygous for lethal alleles, such alleles would be removed slowly by natural selection during the generations of a simulation. This reduces the genetic variation present in the population relative to the case with no inbreeding depression, but also diminishes the subsequent probability that inbred individuals will be homozygous for a lethal allele. This model gives an optimistic reflection of the impacts of inbreeding on many species, as the median number of lethal equivalents per diploid genome observed for mammalian populations is about three (Ralls *et al.* 1988).

The expression of fully recessive deleterious alleles in inbred organisms is not the only genetic mechanism that has been proposed as a cause of inbreeding depression. Some or most of the effects of inbreeding may be a consequence of superior fitness of heterozygotes (heterozygote advantage or 'heterosis'). In the Heterosis model, all homozygotes have reduced fitness compared with heterozygotes. Juvenile survival is modelled according to the logarithmic model developed by Morton *et al.* (1956):

$$\ln S = A - BF$$

in which S is survival, F is the inbreeding coefficient, A is the logarithm of survival in the absence of inbreeding, and B is a measure of the rate at which survival decreases with inbreeding. B is termed the number of 'lethal equivalents' per haploid genome. The number of lethal equivalents per diploid genome, $2B$, estimates the number of lethal alleles per individual in the population if all deleterious effects of inbreeding were due to recessive lethal alleles. A population in which inbreeding depression is one lethal equivalent per diploid genome may have one recessive lethal allele per individual (as in the Recessive Lethals model, above), it may have two recessive alleles per individual, each of which confer a 50% decrease in survival, or it may have some other combination of recessive deleterious alleles that equate in effect with one lethal allele per individual. Unlike the situation with fully recessive deleterious alleles, natural selection does not remove deleterious alleles at heterotic loci because all alleles are deleterious when homozygous and beneficial when present in heterozygous combination with other alleles. Thus, under the Heterosis model, the impact of inbreeding on survival does not diminish during repeated generations of inbreeding.

Unfortunately, for relatively few species are data available to allow estimation of the effects of inbreeding, and the magnitude of these effects varies considerably among species (Falconer 1981; Ralls *et al.* 1988; Lacy *et al.* 1993). Moreover, whether a Recessive Lethals model or a Heterosis model better describes the underlying mechanism of inbreeding depression and therefore the response to repeated generations of inbreeding is not well-known (Brewer *et al.* 1990), and could be determined empirically only from breeding studies that span many generations. Even without detailed pedigree data from which to estimate the number of lethal equivalents in a population and the underlying nature of the genetic load (recessive alleles or heterosis), applications of PVA must make assumptions about the effects of inbreeding on the population being studied. In some cases, it might be considered appropriate to assume that an inadequately studied species would respond to inbreeding in accord with the median (3·14 lethal equivalents per diploid) reported in the survey by Ralls *et al.* (1988). In other cases, there might be reason to make more optimistic assumptions (perhaps the lower quartile, 0·90 lethal equivalents), or more pessimistic assumptions (perhaps the upper quartile, 5·62 lethal equivalents).

Deterministic Processes

VORTEX can incorporate several deterministic processes. Reproduction can be specified to be density-dependent. The function relating the proportion of adult females breeding each year to the total population size is modelled as a fourth-order polynomial, which can provide a close fit to most plausible density-dependence curves. Thus, either positive population responses to low-density or negative responses (e.g. Allee effects), or more complex relationships, can be modelled.

Populations can be supplemented or harvested for any number of years in each simulation. Harvest may be culling or removal of animals for translocation to another (unmodelled) population. The numbers of additions and removals are specified according to the age and sex of animals. Trends in the carrying capacity can also be modelled in VORTEX, specified as an annual percentage change. These changes are modelled as linear, rather than geometric, increases or decreases.

Migration among Populations

VORTEX can model up to 20 populations, with possibly distinct population parameters. Each pairwise migration rate is specified as the probability of an individual moving from one population to another. This probability is independent of the age and sex. Because of between-population migration and managed supplementation, populations can be recolonised. VORTEX tracks the dynamics of local extinctions and recolonisations through the simulation.

Output

VORTEX outputs (1) probability of extinction at specified intervals (e.g., every 10 years during a 100-year simulation), (2) median time to extinction if the population went extinct in at least 50% of the simulations, (3) mean time to extinction of those simulated populations that became extinct, and (4) mean size of, and genetic variation within, extant populations (see Appendix and Lindenmayer *et al.* 1993).

Standard deviations across simulations and standard errors of the mean are reported for population size and the measures of genetic variation. Under the assumption that extinction of independently replicated populations is a binomial process, the standard error of the probability of extinction (SE) is reported by VORTEX as

$$SE(p) = \sqrt{[p \times (1-p)/n]}\,,$$

in which the frequency of extinction was p over n simulated populations. Demographic and genetic statistics are calculated and reported for each subpopulation and for the metapopulation.

Availability of the VORTEX Simulation Program

VORTEX Version 5.1 is written in the C programming language and compiled with the Lattice 80286C Development System (Lattice Inc.) for use on microcomputers using the MS-DOS (Microsoft Corp.) operating system. Copies of the compiled program and a manual for its use are available for nominal distribution costs from the Captive Breeding Specialist Group (Species Survival Commission, IUCN), 12101 Johnny Cake Ridge Road, Apple Valley, Minnesota 55124, U.S.A. The program has been tested by many workers, but cannot be guaranteed to be error-free. Each user retains responsibility for ensuring that the program does what is intended for each analysis.

Sequence of Program Flow

(1) The seed for the random number generator is initialised with the number of seconds elapsed since the beginning of the 20th century.

(2) The user is prompted for input and output devices, population parameters, duration of simulation, and number of interations.

(3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as

$$N_{max} = (K + 3s) \times (1 + L)$$

in which K is the maximum carrying capacity (carrying capacity can be specified to change linearly for a number of years in a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size. It is theoretically possible, but very unlikely, that a simulated population will exceed the calculated N_{max}. If this occurs then the program will give an error message and abort.

(4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{max}. Because N_{max} is often several-fold greater than the likely maximum population size in a simulation, a warning it has been adjusted downward because of limiting memory often will not hamper the analyses. Except for limitations imposed by the size of the computer memory (VORTEX can use extended memory, if available), the only limit to the size of the analysis is that no more than 20 populations exchanging migrants can be simulated.

(5) The expected mean growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (Ricklefs 1979). Generation time and the expected stable age distribution are also estimated. Life-table estimations assume no limitation by carrying capacity, no limitation of mates, and no loss of fitness due to inbreeding depression, and the estimated intrinsic growth rate assumes that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life-table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

(6) Iterative simulation of the population proceeds via steps 7–26 below. For exploratory modelling, 100 iterations are usually sufficient to reveal gross trends among sets of simulations with different input parameters. For more precise examination of population behaviour under various scenarios, 1000 or more simulations should be used to minimise standard errors around mean results.

(7) The starting population is assigned an age and sex structure. The user can specify the exact age–sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.

(8) Two unique alleles at a hypothetical genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. VORTEX therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy–Weinberg equilibrium, is given by

$$H_e = 1 - \Sigma(p_i^2)\,,$$

in which p_i is the frequency of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed heterozygosity of 1·0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity by means of random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (assuming that the initial value was not zero) (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by VORTEX is the mean inbreeding coefficient of the population.

(9) The user specifies one of three options for modelling the effect of inbreeding: (a) no effect of inbreeding on fitness, that is, all alleles are selectively neutral, (b) each founder individual has one unique lethal and one unique non-lethal allele (Recessive Lethals option), or (c) first-year survival of each individual is exponentially related to its inbreeding coefficient (Heterosis option). The first case is clearly an optimistic one, as almost all diploid

populations studied intensively have shown deleterious effects of inbreeding on a variety of fitness components (Wright 1977; Falconer 1981). Each of the two models of inbreeding depression may also be optimistic, in that inbreeding is assumed to have an impact only on first-year survival. The Heterosis option allows, however, for the user to specify the severity of inbreeding depression on juvenile survival.

(10) Years are iterated via steps 11–25 below.

(11) The probabilities of females producing each possible litter size are adjusted to account for density dependence of reproduction (if any).

(12) Birth rate, survival rates and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percentage of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates for their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) of the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for linear changes over time. Environmental variation in K is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.

(13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.

(14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of breeding-age males specified to be breeding.

(15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified sex ratio at birth. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

(16) If the Heterosis option is chosen for modelling inbreeding depression, the genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between a new animal, A, and another existing animal, B is

$$f_{AB}=0\cdot 5\times(f_{MB}+f_{PB})$$

in which f_{ij} is the kinship between animals i and j, M is the mother of A, and P is the father of A. The inbreeding coefficient of each animal is equal to the kinship between its parents, $F=f_{MP}$, and the kinship of an animal to itself is $f_{AA}=0\cdot 5\times(1+F)$. [See Ballou (1983) for a detailed description of this method for calculating inbreeding coefficients.]

(17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If the Heterosis model of inbreeding depression is used and an individual is inbred, the survival probability is multiplied by e^{-bF} in which b is the number of lethal equivalents per haploid genome.

If the Recessive Lethals model is used, all offspring that are homozygous for a lethal allele are killed.

(18) The age of each animal is incremented by 1, and any animal exceeding the maximum age is killed.

(19) If more than one population is being modelled, migration among populations occurs stochastically with specified probabilities.

(20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age–sex class, VORTEX continues but reports that harvest was incomplete.

(21) Dead animals are removed from the computer memory to make space for future generations.

(22) If population supplementation is to occur in a particular year, new individuals of the specified age class are created. Each immigrant is assigned two unique alleles, one of which will be a recessive lethal in the Recessive Lethals model of inbreeding depression. Each immigrant is assumed to be genetically unrelated to all other individuals in the population.

(23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.

(24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to $(N-K)/N$, so that the expected population size after the additional mortality is K.

(25) Summary statistics on population size and genetic variation are tallied and reported. A simulated population is determined to be extinct if one of the sexes has no representatives.

(26) Final population size and genetic variation are determined for the simulation.

(27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate, are calculated across iterations and printed out.

Assumptions Underpinning VORTEX

It is impossible to simulate the complete range of complex processes that can have an impact on wild populations. As a result there are necessarily a range of mathematical and biological assumptions that underpin any PVA program. Some of the more important assumptions in VORTEX include the following.

(1) Survival probabilities are density independent when population size is less than carrying capacity. Additional mortality imposed when the population exceeds K affects all age and sex classes equally.

(2) The relationship between changes in population size and genetic variability are examined for only one locus. Thus, potentially complex interactions between genes located on the same chromosome (linkage disequilibrium) are ignored. Such interactions are typically associated with genetic drift in very small populations, but it is unknown if, or how, they would affect population viability.

(3) All animals of reproductive age have an equal probability of breeding. This ignores the likelihood that some animals within a population may have a greater probability of breeding successfully, and breeding more often, than other individuals. If breeding is not at random among those in the breeding pool, then decay of genetic variation and inbreeding will occur more rapidly than in the model.

(4) The life-history attributes of a population (birth, death, migration, harvesting, supplementation) are modelled as a sequence of discrete and therefore seasonal events. However, such events are often continuous through time and the model ignores the possibility that they may be aseasonal or only partly seasonal.

(5) The genetic effects of inbreeding on a population are determined in VORTEX by using one of two possible models: the Recessive Lethals model and the Heterosis model. Both models have attributes likely to be typical of some populations, but these may vary within and between species (Brewer *et al.* 1990). Given this, it is probable that the impacts of inbreeding will fall between the effects of these two models. Inbreeding is assumed to depress only one component of fitness: first-year survival. Effects on reproduction could be incorporated into this component, but longer-term impacts such as increased disease susceptibility or decreased ability to adapt to environmental change are not modelled.

(6) The probabilities of reproduction and mortality are constant from the age of first breeding until an animal reaches the maximum longevity. This assumes that animals continue to breed until they die.

(7) A simulated catastrophe will have an effect on a population only in the year that the event occurs.

(8) Migration rates among populations are independent of age and sex.

(9) Complex, interspecies interactions are not modelled, except in that such community dynamics might contribute to random environmental variation in demographic parameters. For example, cyclical fluctuations caused by predator–prey interactions cannot be modelled by VORTEX.

Discussion

Uses and Abuses of Simulation Modelling for PVA

Computer simulation modelling is a tool that can allow crude estimation of the probability of population extinction, and the mean population size and amount of genetic diversity, from data on diverse interacting processes. These processes are too complex to be integrated intuitively and no analytic solutions presently, or are likely to soon, exist. PVA modelling focuses on the specifics of a population, considering the particular habitat, threats, trends, and time frame of interest, and can only be as good as the data and the assumptions input to the model (Lindenmayer *et al.* 1993). Some aspects of population dynamics are not modelled by VORTEX nor by any other program now available. In particular, models of single-species dynamics, such as VORTEX, are inappropriate for use on species whose fates are strongly determined by interactions with other species that are in turn undergoing complex (and perhaps synergistic) population dynamics. Moreover, VORTEX does not model many conceivable and perhaps important interactions among variables. For example, loss of habitat might cause secondary changes in reproduction, mortality, and migration rates, but ongoing trends in these parameters cannot be simulated with VORTEX. It is important to stress that PVA does not predict in general what will happen to a population; PVA forecasts the likely effects only of those factors incorporated into the model.

Yet, the use of even simplified computer models for PVA can provide more accurate predictions about population dynamics than the even more crude techniques available previously, such as calculation of expected population growth rates from life tables. For the purpose of estimating extinction probabilities, methods that assess only deterministic factors are almost certain to be inappropriate, because populations near extinction will commonly be so small that random processes dominate deterministic ones. The suggestion by Mace and Lande (1991) that population viability be assessed by the application of simple rules (e.g., a taxon be considered Endangered if the total effective population size is below 50 or the total census size below 250) should be followed only if knowledge is insufficient to allow more accurate quantitative analysis. Moreover, such preliminary judgments, while often important in stimulating appropriate corrective measures, should signal, not obviate, the need for more extensive investigation and analysis of population processes, trends and threats.

Several good population simulation models are available for PVA. They differ in capabilities, assumptions and ease of application. The ease of application is related to the number of simplifying assumptions and inversely related to the flexibility and power of the model. It is unlikely that a single or even a few simulation models will be appropriate for all PVAs. The VORTEX program has some capabilities not found in many other population simulation programs, but is not as flexible as are some others (e.g., GAPPS; Harris *et al.* 1986). VORTEX is user-friendly and can be used by those with relatively little understanding of population biology and extinction processes, which is both an advantage and a disadvantage.

Testing Simulation Models

Because many population processes are stochastic, a PVA can never specify what will happen to a population. Rather, PVA can provide estimates of probability distributions describing possible fates of a population. The fate of a given population may happen to fall at the extreme tail of such a distribution even if the processes and probabilities are assessed precisely. Therefore, it will often be impossible to test empirically the accuracy of PVA results by monitoring of one or a few threatened populations of interest. Presumably, if a population followed a course that was well outside of the range of possibilities predicted by a model, that model could be rejected as inadequate. Often, however, the range of plausible fates generated by PVA is quite broad.

Simulation programs can be checked for internal consistency. For example, in the absence of inbreeding depression and other confounding effects, does the simulation model predict an average long-term growth rate similar to that determined from a life-table calculation? Beyond this, some confidence in the accuracy of a simulation model can be obtained by comparing observed fluctuations in population numbers to those generated by the model, thereby comparing a data set consisting of tens to hundreds of data points to the results of the model. For example, from 1938 to 1991, the wild population of whooping cranes had grown at a mean exponential rate, r, of 0·040, with annual fluctuations in the growth rate, SD (r), of 0·141 (Mirande *et al.* 1993). Life-table analysis predicted an r of 0·052. Simulations using VORTEX predicted an r of 0·046 into the future, with a SD (r) of 0·081. The lower growth rate projected by the stochastic model reflects the effects of inbreeding and perhaps imbalanced sex ratios among breeders in the simulation, factors that are not considered in deterministic life-table calculations. Moreover, life-table analyses use mean birth and death rates to calculate a single estimate of the population growth rate. When birth and death rates are fluctuating, it is more appropriate to average the population growth rates calculated separately from birth and death rates for each year. This mean growth rate would be lower than the growth rate estimated from mean life-table values.

When the simulation model was started with the 18 cranes present in 1938, it projected a population size in 1991 ($N \pm \text{SD} = 151 \pm 123$) almost exactly the same as that observed ($N = 146$). The large variation in population size across simulations, however, indicates that very different fates (including extinction) were almost equally likely. The model slightly underestimated the annual fluctuations in population growth [model SD (r) = 0·112 *v.* actual SD (r) = 0·141]. This may reflect a lack of full incorporation of all aspects of stochasticity into the model, or it may simply reflect the sampling error inherent in stochastic phenomena. Because the data input to the model necessarily derive from analysis of past trends, such retrospective analysis should be viewed as a check of consistency, not as proof that the model correctly describes current population dynamics. Providing another confirmation of consistency, both deterministic calculations and the simulation model project an over-wintering population of whooping cranes consisting of 12% juveniles (less than 1 year of age), while the observed frequency of juveniles at the wintering grounds in Texas has averaged 13%.

Convincing evidence of the accuracy, precision and usefulness of PVA simulation models would require comparison of model predictions to the distribution of fates of many replicate populations. Such a test probably cannot be conducted on any endangered species, but could and should be examined in experimental non-endangered populations. Once simulation models are determined to be sufficiently descriptive of population processes, they can guide management of threatened and endangered species (see above and Lindenmayer *et al.* 1993). The use of PVA modelling as a tool in an adaptive management framework (Clark *et al.* 1990) can lead to increasingly effective species recovery efforts as better data and better models allow more thorough analyses.

Directions for Future Development of PVA Models

The PVA simulation programs presently available model life histories as a series of discrete (seasonal) events, yet many species breed and die throughout much of the year. Continuous-time models would be more realistic and could be developed by simulating the time between life-history events as a random variable. Whether continuous-time models would significantly improve the precision of population viability estimates is unknown. Even more realistic models might treat some life-history events (e.g., gestation, lactation) as stages of specified duration, rather than as instantaneous events.

Most PVA simulation programs were designed to model long-lived, low fecundity (K-selected) species such as mammals, birds and reptiles. Relatively little work has been devoted to developing models for short-lived, high-fecundity (r-selected) species such as many amphibians and insects. Yet, the viability of populations of r-selected species may be highly affected by stochastic phenomena, and r-selected species may have much greater minimum viable populations than do most K-selected species. Assuring viability of K-selected species in a community may also afford adequate protection for r-selected species, however, because of the often greater habitat-area requirements of large vertebrates. Populations of r-selected species are probably less affected by intrinsic demographic stochasticity because large numbers of progeny will minimise random fluctuations, but they are more affected by environmental variations across space and time. PVA models designed for r-selected species would probably model fecundity as a continuous distribution, rather than as a completely specified discrete distribution of litter or clutch sizes; they might be based on life-history stages rather than time-increment ages; and they would require more detailed and accurate description of environmental fluctuations than might be required for modelling K-selected species.

The range of PVA computer simulation models becoming available is important because the different assumptions of the models provide capabilities for modelling diverse life histories. Because PVA models always simplify the life history of a species, and because the assumptions of no model are likely to match exactly our best understanding of the dynamics of a population of interest, it will often be valuable to conduct PVA modelling with several simulation programs and to compare the results. Moreover, no computer program can be guaranteed to be free of errors. There is a need for researchers to compare results from different PVA models when applied to the same analysis, to determine how the different assumptions affect conclusions and to cross-validate algorithms and computer code.

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Appendix. Sample Output from VORTEX

Explanatory comments are added in italics

```
VORTEX—simulation of genetic and demographic stochasticity
TEST                                          Simulation label and output file name
Fri Dec 20 09:21:18 1991
  2 population(s) simulated for 100 years, 100 runs
```

VORTEX first lists the input parameters used in the simulation:

```
  HETEROSIS model of inbreeding depression
    with 3·14 lethal equivalents per diploid genome
  Migration matrix:
            1        2
    1  0·9900   0·0100                     i.e. 1% probability of migration from
    2  0·0100   0·9900              Population 1 to 2, and from Population 2 to 1
  First age of reproduction for females: 2   for males: 2
  Age of senescence (death): 10
  Sex ratio at birth (proportion males): 0·5000
Population 1:
  Polygynous mating; 50·00 per cent of adult males in the breeding pool.
  Reproduction is assumed to be density independent.
    50·00 (EV=12·50 SD) per cent of adult females produce litters of size 0
    25·00 per cent of adult females produce litters of size 1
    25·00 per cent of adult females produce litters of size 2
```

EV is environmental variation

```
    50·00 (EV=20·41 SD) per cent mortality of females between ages 0 and 1
    10·00 (EV=3·00 SD) per cent mortality of females between ages 1 and 2
    10·00 (EV=3·00 SD) per cent annual mortality of adult females (2<=age<=10)
    50·00 (EV=20·41 SD) per cent mortality of males between ages 0 and 1
    10·00 (EV=3·00 SD) per cent mortality of males between ages 1 and 2
    10·00 (EV=3·00 SD) per cent annual mortality of adult males (2<=age<=10)
```

```
EVs have been adjusted to closest values possible for binomial distribution.
   EV in reproduction and mortality will be correlated.
   Frequency of type 1 catastrophes: 1·000 per cent
     with 0·500 multiplicative effect on reproduction
      and 0·750 multiplicative effect on survival
   Frequency of type 2 catastrophes: 1·000 per cent
     with 0·500 multiplicative effect on reproduction
      and 0·750 multiplicative effect on survival
   Initial size of Population 1: (set to reflect stable age distribution)
 Age   1     2     3     4     5     6     7     8     9    10      Total
       1     0     1     1     0     1     0     0     1     0        5  Males
       1     0     1     1     0     1     0     0     1     0        5  Females
    Carrying capacity=50 (EV=0·00 SD)
     with a 10·000 per cent decrease for 5 years.
   Animals harvested from population 1, year 1 to year 10 at 2 year intervals:
     1 females 1 years old
     1 female adults (2<=age<=10)
     1 males 1 years old
     1 male adults (2<=age<=10)
   Animals added to population 1, year 10 through year 50 at 4 year intervals:
     1 females 1 years old
     1 females 2 years old
     1 males 1 years old
     1 males 2 years old
```

Input values are summarised above, results follow.

VORTEX now reports life-table calculations of expected population growth rate.

```
Deterministic population growth rate (based on females, with assumptions of no limitation of mates
  and no inbreeding depression):
     r = −0·001      lambda=0·999      RO=0·997
    Generation time for:  females=5·28  males=5·28
```

Note that the deterministic life-table calculations project approximately zero population growth for this population.

```
Stable age distribution:   Age class    females    males
                               0         0·119     0·119
                               1         0·059     0·059
                               2         0·053     0·053
                               3         0·048     0·048
                               4         0·043     0·043
                               5         0·038     0·038
                               6         0·034     0·034
                               7         0·031     0·031
                               8         0·028     0·028
                               9         0·025     0·025
                              10         0·022     0·022
Ratio of adult (>=2) males to adult (>=2) females: 1·000

Population 2:
```

Input parameters for Population 2 were identical to those for Population 1.
Output would repeat this information from above.

Simulation results follow.

```
Population1
```

```
Year 10
    N[Extinct] =       0, P[E] = 0·000
    N[Surviving] =  100, P[S] = 1·000
    Population size =           4·36  (0·10 SE,  1·01 SD)
    Expected heterozygosity =  0·880 (0·001 SE, 0·012 SD)
    Observed heterozygosity =  1·000 (0·000 SE, 0·000 SD)
    Number of extant alleles = 8·57  (0·15 SE,  1·50 SD)
```

Population summaries given, as requested by user, at 10-year intervals.

```
Year 100
    N[Extinct] =     86, P[E] = 0·860
    N[Surviving] =  14, P[S] = 0·140
    Population size =           8·14  (1·27 SE,  4·74 SD)
    Expected heterozygosity =  0·577 (0·035 SE, 0·130 SD)
    Observed heterozygosity =  0·753 (0·071 SE, 0·266 SD)
    Number of extant alleles = 3·14  (0·35 SE,  1·29 SD)

In 100 simulations of 100 years of Population1:
  86 went extinct and 14 survived.
This gives a probability of extinction of  0·8600 (0·0347 SE),
  or a probability of success of           0·1400 (0·0347 SE).
99 simulations went extinct at least once.
Median time to first extinction was 5 years.
Of those going extinct,
  mean time to first extinction was 7·84 years (1·36 SE, 13·52 SD).
123 recolonisations occurred.
Mean time to recolonisation was 4·22 years (0·23 SE, 2·55 SD).
110 re-extinctions occurred.
Mean time to re-extinction was 54·05 years (2·81 SE, 29·52 SD).
Mean final population for successful cases was 8·14 (1·27 SE, 4·74 SD)
  Age 1    Adults    Total
   0·14     3·86      4·00   Males
   0·36     3·79      4·14   Females

During years of harvest and/or supplementation
  mean growth rate (r) was 0·0889 (0·0121 SE, 0·4352 SD)
Without harvest/supplementation, prior to carrying capacity truncation,
  mean growth rate (r) was  – 0·0267 (0·0026 SE, 0·2130 SD)
```

Population growth in the simulation (r = – 0·0267) was depressed relative to the projected growth rate calculated from the life table (r = – 0·001) because of inbreeding depression and occasional lack of available mates.

```
Note:   497 of 1000 harvests of males and 530 of 1000 harvests of females could not be completed
        because of insufficient animals.

Final expected heterozygosity was     0·5768 (0·0349 SE, 0·1305 SD)
Final observed heterozygosity was     0·7529 (0·0712 SE, 0·2664 SD)
Final number of alleles was           3·14   (0·35 SE,   1·29 SD)

Population2
```

Similar results for Population 2, omitted from this Appendix, would follow.

```
  ********  Metapopulation Summary  ********
Year 10
    N[Extinct] =       0, P[E] = 0·000
    N[Surviving] =  100, P[S] = 1·000
    Population size =           8·65  (0·16 SE,  1·59 SD)
    Expected heterozygosity =  0·939 (0·000 SE, 0·004 SD)
    Observed heterozygosity =  1·000 (0·000 SE, 0·000 SD)
    Number of extant alleles = 16·92 (0·20 SE,  1·96 SD)
```

```
Metapopulation summaries are given at 10-year intervals.
Year 100
     N[Extinct] =    79, P[E] = 0·790
     N[Surviving] =  21, P[S] = 0·210
     Population size =            10·38  (1·37 SE,  6·28 SD)
     Expected heterozygosity =    0·600 (0·025 SE, 0·115 SD)
     Observed heterozygosity =    0·701 (0·050 SE, 0·229 SD)
     Number of extant alleles =   3·57  (0·30 SE,  1·36 SD)

In 100 simulations of 100 years of Metapopulation:
   79 went extinct and 21 survived.
This gives a probability of extinction of   0·7900 (0·0407 SE),
   or a probability of success of           0·2100 (0·0407 SE).
97 simulations went extinct at least once.
Median time to first extinction was 7 years.
Of those going extinct,
   mean time to first extinction was 11·40 years (2·05 SE, 20·23 SD).
91 recolonisations occurred.
Mean time to recolonisation was 3·75 years (0·15 SE, 1·45 SD).
73 re-extinctions occurred.
Mean time to re-extinction was 76·15 years (1·06 SE, 9·05 SD).

Mean final population for successful cases was 10·38 (1·37 SE, 6·28 SD)
   Age 1     Adults     Total
    0·48      4·71       5·19   Males
    0·48      4·71       5·19   Females

During years of harvest and/or supplementation
   mean growth rate (r) was 0·0545 (0·0128 SE, 0·4711 SD)
Without harvest/supplementation, prior to carrying capacity truncation,
   mean growth rate (r) was  −0·0314 (0·0021 SE, 0·1743 SD)

Final expected heterozygosity was   0·5997 (0·0251 SE, 0·1151 SD)
Final observed heterozygosity was   0·7009 (0·0499 SE, 0·2288 SD)
Final number of alleles was         3·57   (0·30 SE,   1·36 SD)
```

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Sample Input File

```
15n40b3i.out     ***Output Filename***
Y     ***Graphing Files?***
N     ***Each Iteration?***
500     ***Simulations***
100    ***Years***
10 .   ***Reporting Interval***
1     ***Populations***
Y     ***Inbreeding Depression?***
H     ***Heterosis Or Lethals***
0.30000     ***Lethal Equivalents***
Y     ***EV correlation?***
2     ***Types Of Catastrophes***
P     ***Monogamous Or Polygynous***
6     ***Female Breeding Age***
8     ***Male Breeding Age***
22     ***Maximum Age***
0.500000     ***Sex Ratio***
1     ***Maximum Litter Size***
N     ***Density Dependent Breeding?***
60.000000     ***Population 1: Percent Litter Size 0***
40.000000     ***Population 1: Percent Litter Size 1***
10.000000     ***EV--Reproduction***
5.000000     ***Female Mortality At Age 0***
1.700000     ***EV--FemaleMortality***
5.000000     ***Female Mortality At Age 1***
1.700000     ***EV--FemaleMortality***
5.000000     ***Female Mortality At Age 2***
1.700000     ***EV--FemaleMortality***
5.000000     ***Female Mortality At Age 3***
1.700000     ***EV--FemaleMortality***
5.000000     ***Female Mortality At Age 4***
1.700000     ***EV--FemaleMortality***
5.000000     ***Female Mortality At Age 5***
1.700000     ***EV--FemaleMortality***
3.400000     ***Adult Female Mortality***
1.700000     ***EV--AdultFemaleMortality***
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5.000000    ***Male Mortality At Age 0***
1.700000    ***EV--MaleMortality***
5.000000    ***Male Mortality At Age 1***
1.700000    ***EV--MaleMortality***
5.000000    ***Male Mortality At Age 2***
1.700000    ***EV--MaleMortality***
5.000000    ***Male Mortality At Age 3***
1.700000    ***EV--MaleMortality***
5.000000    ***Male Mortality At Age 4***
1.700000    ***EV--MaleMortality***
5.000000    ***Male Mortality At Age 5***
1.700000    ***EV--MaleMortality***
5.000000    ***Male Mortality At Age 6***
1.700000    ***EV--MaleMortality***
5.000000    ***Male Mortality At Age 7***
1.700000    ***EV--MaleMortality***
8.000000    ***Adult Male Mortality***
4.000000    ***EV--AdultMaleMortality***
2.000000    ***Probability Of Catastrophe 1***
1.000000    ***Severity--Reproduction***
0.750000    ***Severity--Survival***
5.000000    ***Probability Of Catastrophe 2***
1.000000    ***Severity--Reproduction***
0.750000    ***Severity--Survival***
N    ***All Males Breeders?***
Y    ***Answer--A--Known?***
75.000000    ***Percent Males In Breeding Pool***
Y    ***Start At Stable Age Distribution?***
15    ***Initial Population Size***
70    ***K***
0.000000    ***EV--K***
Y    ***Trend In K?***
10    ***Years Of Trend***
-1.000000    ***Percent Change In K***
N    ***Harvest?***
N    ***Supplement?***
y    ***AnotherSimulation?***

15n30b3i.out    ***Output Filename***
Y    ***Graphing Files?***
N    ***Each Iteration?***
500    ***Simulations***
100    ***Years***
10    ***Reporting Interval***
1    ***Populations***
Y    ***Inbreeding Depression?***
H    ***Heterosis Or Lethals***
0.30000    ***Lethal Equivalents***
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Y     ***EV correlation?***
2     ***Types Of Catastrophes***
P     ***Monogamous Or Polygynous***
6     ***Female Breeding Age***
8     ***Male Breeding Age***
22     ***Maximum Age***
0.500000     ***Sex Ratio***
1     ***Maximum Litter Size***
N     ***Density Dependent Breeding?***
70.000000     ***Population 1: Percent Litter Size 0***
30.000000     ***Population 1: Percent Litter Size 1***
10.000000     ***EV--Reproduction***
5.000000     ***Female Mortality At Age 0***
1.700000     ***EV--FemaleMortality***
5.000000     ***Female Mortality At Age 1***
1.700000     ***EV--FemaleMortality***
5.000000     ***Female Mortality At Age 2***
1.700000     ***EV--FemaleMortality***
5.000000     ***Female Mortality At Age 3***
1.700000     ***EV--FemaleMortality***
5.000000     ***Female Mortality At Age 4***
1.700000     ***EV--FemaleMortality***
5.000000     ***Female Mortality At Age 5***
1.700000     ***EV--FemaleMortality***
3.400000     ***Adult Female Mortality***
1.700000     ***EV--AdultFemaleMortality***
5.000000     ***Male Mortality At Age 0***
1.700000     ***EV--MaleMortality***
5.000000     ***Male Mortality At Age 1***
1.700000     ***EV--MaleMortality***
5.000000     ***Male Mortality At Age 2***
1.700000     ***EV--MaleMortality***
5.000000     ***Male Mortality At Age 3***
1.700000     ***EV--MaleMortality***
5.000000     ***Male Mortality At Age 4***
1.700000     ***EV--MaleMortality***
5.000000     ***Male Mortality At Age 5***
1.700000     ***EV--MaleMortality***
5.000000     ***Male Mortality At Age 6***
1.700000     ***EV--MaleMortality***
5.000000     ***Male Mortality At Age 7***
1.700000     ***EV--MaleMortality***
8.000000     ***Adult Male Mortality***
4.000000     ***EV--AdultMaleMortality***
2.000000     ***Probability Of Catastrophe 1***
1.000000     ***Severity--Reproduction***
0.750000     ***Severity--Survival***
5.000000     ***Probability Of Catastrophe 2***
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1.000000    ***Severity--Reproduction***
0.750000    ***Severity--Survival***
N    ***All Males Breeders?***
Y    ***Answer--A--Known?***
75.000000    ***Percent Males In Breeding Pool***
Y    ***Start At Stable Age Distribution?***
15    ***Initial Population Size***
70    ***K***
0.000000    ***EV--K***
Y    ***Trend In K?***
10    ***Years Of Trend***
-1.000000    ***Percent Change In K***
N    ***Harvest?***
N    ***Supplement?***
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