KENYA BLACK RHINOCEROS

METAPOPULATION WORKSHOP

BRIEFING BOOK

SECTION 9
REFERENCE MATERIALS

The Population Viability Assessment Workshop: A Tool For Threatened Species Management

by
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Introduction

Population viability assessment (PVA) is a procedure that allows managers to simulate, using computer models, extinction processes that act on small populations and therefore assess their long-term viability. In both real and simulated populations, a number of interacting demographic, genetic, environmental, and catastrophic processes determine the vulnerability of a population to extinction. These four types of extinction processes can be simulated in computer models and the effects of both deterministic and stochastic forces can be explored. In turn, the outcome of various management options, such as reducing mortality, supplementing the population, and increasing carrying capacity can also be simulated. Thus, PVA provides managers with a powerful tool to aid in assessing the viability of small populations and in setting target numbers for species recovery as a basis for planning and carrying out recovery programs. In addition, having performance-based management programs enables progress to be quantified and assessed. PVA also offers managers a powerful strategic planning and policy tool when vying for limited financial resources. This paper describes a PVA workshop that used a stochastic computer simulation to model small populations of, and explore management options for, six threatened/endangered wildlife species in Victoria, Australia.

The Workshop

The workshop was co-sponsored by the Department of Conservation and Environment (DCE), Victoria, and the Zoological Board of Victoria (ZBV), in cooperation with the Chicago Zoological Society (CZS) and was held at the Arthur Rylah Institute for Environmental Research (DCE), Heidelberg, Victoria, from May 28 through June 1, 1990.

The objectives of the workshop were to: 1) examine the adequacy of data on the six threatened species; 2) simulate the vulnerability to extinction by using PVA; 3) examine outcomes of various management options to restore the species; 4) estimate population targets needed for recovery planning; 5) evaluate the potential of PVA as a teaching aid to illustrate extinction processes and management options.

Mountain pygmy-possum Photo by Ian McPherson

The six species were: mountain pygmy-possum, *Burramys parvus*; leadbeater's possum, *Gymnobelideus leadbeateri*; eastern barred bandicoot, *Perameles gunnii*; long-footed potoroo, *Potorous longipes*; orange-bellied parrot, *Neophema chrysogaster*, and helmeted honeyeater, *Lichenostomus melanops cassidix*.

The 32 people attending the workshop represented experienced field biologists and wildlife managers with detailed knowledge of these and other threatened species. A month prior to the workshop all participants were provided with background reading material (e.g. Shaffer 1981, Brussard 1985, Samson 1985, Gilpin 1989, and Lacy and Clark 1990). A questionnaire on life-history parameters to be completed on each species as a basis for entering values into the computer was also provided. Following an introduction and overview of PVA, the participants formed teams and commenced work. Simulations, analyses, and discussions were ongoing over the next five days. The first week concluded with a report and review of each team's progress. During the following week, teams further refined their simulations and commenced preparation of a final report with management recommendations.

Population Viability Analysis: The Vortex Model

The workshop used a computer program, VORTEX, to simulate demographic and genetic events in the history of a small population (<500 individuals). VORTEX was written in the C programming language by Robert Lacy for use on MS-DOS microcomputers. Many of the algorithms in VORTEX were taken from a simulation program, SPGPC, written in BASIC by James Grier (Grier 1980a, 1980b, Grier and Barclay 1988). See Lacy et al. 1989, Seal and Lacy 1989 and Lacy and Clark 1990 for earlier uses of VORTEX.

Life table analyses yield average long-term projections of population growth (or decline), but do not reveal the fluctuations in population size that

would result from variability in demographic processes. When a population is small and isolated from other populations of conspecifics, these random fluctuations can lead to extinction, even in populations that have positive population growth on average. Fluctuations in population size can result from several levels of stochastic effects. Demographic variation results from the probabilistic nature of birth and death processes. Therefore, even if the probability of an animal reproducing or dying is always constant, the actual number reproducing or dying within any time interval would vary according to the binomial distribution with mean equal to the probability of the event (p), and variance given by Vp = p*(1-p)/N. Demographic variation is thus intrinsic to the population and occurs in the simulation because birth and death events are determined by a random process (with appropriate probabilities). Environmental variation (EV) is the variation in the probabilities of reproduction and mortality that occur because of changes in the environment on an annual basis (or other timescales).

VORTEX models population processes as discrete, sequential events, with probabilistic outcomes determined by a pseudo-random number generator. 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, whether each adult female produces broods of size 0, 1, 2, 3, 4, or 5 during each year, and which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Mortality and reproduction probabilities are sex-specific. Mortality rates are specified for each pre-reproductive age class and for reproductive-age animals. Fecundity is assumed to be independent of age after an animal reaches reproductive age. The mating system can be specified to be either monogamous or polygynous. In either case, the user can specify that only a subset of the adult male population is in the breeding pool (the remainder being excluded perhaps by social factors). Those males in the breeding pool all have equal probability of siring offspring.

Each simulation is started with a specified number of males and females in each pre-reproductive age class and the breeding age class. Each animal in the initial population is assigned two unique alleles at some hypothetical genetic locus. The user specifies the severity of inbreeding depression which is expressed in the model as a loss of viability in inbred animals. The computer program simulates and tracks the fate of each population and then produces summary statistics on: the probability of population extinction over specified time intervals; the mean time to extinction of those simulated populations that went extinct; the mean size of populations not yet extinct; and the levels of genetic variation remaining in any extant populations.

A population carrying capacity specified by the user is imposed by a probabilistic truncation of each age class if, after breeding, the population size exceeds the specified carrying capacity. The program allows the user to model trends in the carrying capacity, as linear increases or decreases across a specified number of years.

VORTEX models environmental variation simplistically (which is both an advantage and disadvantage of simulation modelling), by selecting at the beginning of each year the population age-specific birth rates, age-specific death rates, and carrying capacity from distributions with means equal to the overall averages specified by the user, and with variances also specified by the user. Unfortunately, rarely do we have sufficient field data to estimate the fluctuations in birth and death rates, and in carrying capacity, for a wild population. The population would have to be monitored long enough to separate sampling error statistically from demographic variation in the number of births and deaths, from annual variation in the probabilities of these events. Such variation can be very important in determining the probability of extinction, yet we rarely have reasonable estimates for most populations of conservation concern. If data on annual variation are lacking, a user can try various values, or model the fate of the population in the absence of any environmental variation.

Endangered Species UPDATE

A forum for information exchange on endangered species issues
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Alice Clarke and Joel Heinen...Editors
Dr. Terry Root.....Faculty Advisor
Jon Jensen.....Staff Advisor

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Cover:
Leadbeater's possum
(*Gymnobelideus leadbeateri*)
Photo by Jim Cooper

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VORTEX can model catastrophes as events that occur with some specified probability and which reduce survival and reproduction for one year. A catastrophe is determined to occur if a randomly generated number between 0 and 1 is less than the probability of occurrence (i.e. a binomial process is simulated). If a catastrophe occurs, the probability of breeding is multiplied by a severity factor that is drawn from a binomial distribution with a mean equal to the severity specified by the user. Similarly, the probability of survival for each age class is estimated in a similar manner.

VORTEX also allows the user to supplement or harvest the population for any number of years in each simulation. The numbers of immigrants and removals are specified by age and sex. VORTEX outputs the observed rate of population growth (mean of N[t]/N[t-1]) separately for the years of supplementation/harvest and for the years without such management, and allows for reporting of extinction probabilities and population sizes at whatever time interval is desired (e.g. summary statistics can be given at 5-year intervals in a 100-year simulation).

Overall, the computer program simulates many of the complex levels of stochasticity that can affect a population. Because it is a detailed model of population dynamics, often it is not practical to examine all possible factors and all interactions that may affect a population. The user, therefore, must specify those parameters that can be estimated reasonably, leave out of the model those that are thought not to have a substantial impact on the population of interest, and explore a range of possible values for parameters that are potentially important but very imprecisely known. A companion program, VORPLOTS, was used at the workshop to produce plots of mean population size, time to extinction, and loss of gene diversity from simulation results.

Equipment Required

VORTEX requires an MS-DOS microcomputer with at least 640K of memory. A math co-processor speeds up the program substantially. The VORPLOTS plotting program produces files in the Hewlett Packard Graphics Language (HPGL), for use on an HP plotter or equivalent.

A Kodak Dataview EGA enabled projection of a computer display via an overhead projector onto a large screen so that all participants could observe demonstrations of VORTEX during initial training.

Computers were used during the daily sessions primarily for exploratory analyses with relatively few runs (100 or fewer) of a simulation; more extensive analyses were run overnight. A test with 100 runs would take from 15 minutes to 3 hours, depending on the machine used and the size of the population being simulated.

The Workshop Results

Each team documented its activities and provided a preliminary report of the simulations completed, conclusions, an assessment of the conduct of the workshop, and the usefulness of the PVA process. Results will be published in peer-reviewed scientific journals by each team.

All cases showed similar results. First, most species and populations were highly susceptible to local extinction. Any further habitat loss or fragmentation or reduction in population size and density would result in rapid extinction. Second, in all cases, more field data would have been helpful. Third, management options to stave off extinction were identified and results simulated. Options included strict habitat protection, enhancement of existing habitat or restoration of lost habitat, captive breeding, and reintroduction of animals to existing habitat patches in which the species has become extinct in recent decades or to newly created habitat. Various combinations of management strategies were recommended for future management. Fourth, the simulations demonstrated that if proactive conservation management had been undertaken even 5 to 10 years ago when populations and habitats were considerably larger, the task of present day managers would be much more tractable. And fifth, improved conservation management for all six species is expected to result from the PVA exercise, enhanced research, and subsequent on-the-ground management. Three cases illustrate these conclusions: the mountain pygmy-possum (Mansergh et al. in prep.), eastern barred bandicoot (Myroniuk and Patrick in prep.), and orange-bellied parrot (Brown et al. in prep.).

Mountain Pygmy-Possum: The mountain pygmy-possum is a small marsupial restricted to alpine and subalpine (>1500m altitude) rock screes and boulderfields with heathlands. The species has been well studied and much information is available on its ecology (Mansergh 1989). Diet consists of invertebrates, seeds, and fruits. Breeding occurs from September to December, with litter size of 3 to 4. The young become independent by mid-January. Females can breed in their first year, and can live up to 9 years. An unusual feature of the life history of *Burramys* is the fact that sexes are segregated during the non-breeding season. The adult population is heavily biased towards females (6F:1M) because of the very high mortality experienced by males post-dispersal.

The current total population is estimated to be 2,300 breeding adults of which 80% are females. The species is regarded as vulnerable in Victoria and rare in New South Wales. The species is also susceptible to climatic changes associated with global warming.

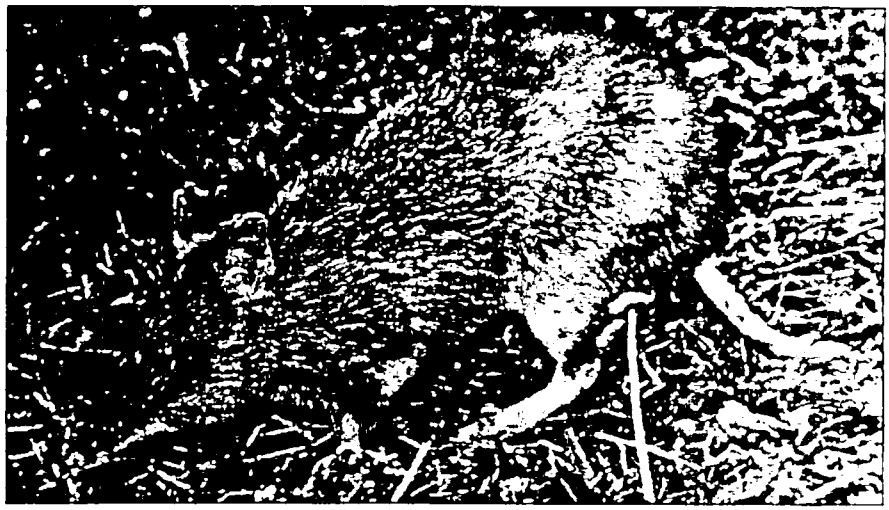
The mountain pygmy-possum exists as a number of discrete populations isolated from each other on mountain tops. A total of seven populations, ranging from 20-850 individuals (representing the situation in the wild) was modelled. High probabilities of extinction were observed in all small (<150 animals) populations at 25 and 50 years; this could account for the absence of the species from apparently suitable habitat within its range. The larger populations had a decreased likelihood of extinction. When modelled with a small but steady decrease in carrying capacity (1% per annum) such as could occur through climatic change with global warming, the probability of extinction increased greatly (to 45% in the case of the largest Victorian population of 850 individuals, over 50 years).

(Continued on UPDATE page 4)

Disturbance to habitat and further fragmentation of populations would increase the likelihood of extinction.

Eastern Barred Bandicoot: The mainland population of this marsupial species was formerly distributed over about 23,000 sq km of volcanic grassland in western Victoria. This population has now declined to 200 or fewer individuals restricted to remnant habitat near Hamilton (Clark and Seebeck 1990). The species is polygynous, with females capable of breeding from 3 months of age and males from 4 months of age. Gestation lasts about 12 days, with litters comprised of 1 to 5 offspring (usually 2-3); young remain in the pouch about 55 days. Females are capable of producing several broods per year. In spite of the very high reproductive potential, the population is believed to be declining at about 25% per annum. Juvenile mortality at dispersal from the nest is very high (> 90% within the first year). The decline of the species is attributed to habitat modification from pastoral activities and predation from introduced predators, including the red fox (*Vulpes vulpes*) and the cat (*Felis catus*).

Wild and captive populations of the eastern barred bandicoot were simulated. Modeling the wild population using available data without any change to current management indicated a 100% probability of extinction within 25 years, with a mean time to extinction of 7.2 years (± 2.1). Doubling the carrying capacity and leaving mortality unchanged had negligible impact on the probability of extinction and increased the mean time to extinction by only 2 years. Doubling the carrying capacity, reducing mortality by 30% and supplementing the wild population with the liberation of captive-bred animals greatly enhanced prospects for survival of the wild population. Under this scenario the probability of extinction was reduced to 0% over 25 years with a mean final population size of close to the carrying capacity of 300 animals. Modeling the existing and proposed captive populations allowed investigation of a variety of scenarios. The existing captive population of 16 pairs has an extinction probability of 83% over 25 years, with a mean time to extinction of 21.5 years. Doubling the number of adult pairs decreased the extinction probability to 0% but the surviving population had very low genetic variability, and there is little potential to harvest juveniles for release into the wild. Increasing the captive population to 62 adult pairs increased genetic variability and the potential to harvest juveniles without jeopardizing the captive population. Maintaining a captive population of 62 adult pairs (in two groups at separate locations to avoid catastrophe but managed as one population) and establishing two semi-captive populations with a capacity for 400 animals gave the best prospects for long term survival, maintenance of genetic variability, and production of sufficient offspring to consider reintroductions to suitable habitat within their former range. The exercise highlighted the need for a combination of management actions, rather than any single action, to prevent the almost certain extinction of the wild population under the existing management regime. Reduction of mortality by predator control and traffic management is essential for the survival of the eastern barred bandicoot. Captive management will be an important part of the recovery program, but with a more intensive program than that currently underway.



Eastern barred bandicoot Photo by J. Seebeck

Orange-bellied Parrot: The biology and ecology of the orange-bellied parrot is comparatively well known (Loyn et al. 1986). The species is one of the rarest and most threatened birds in Australia, with a total population of 150-200 individuals. The orange-bellied parrot breeds in coastal southwest Tasmania in woodlands adjoining extensive sedgelands. After breeding, it migrates across Bass Strait to overwinter in coastal regions of southern mainland Australia. The birds feed in a variety of coastal habitats including grassland, saltmarsh, and dune systems, showing strong preferences for particular habitats and food types in different parts of their winter range and at different times of the year. An estimated 40 breeding pairs annually produce a total of 50-70 juveniles. The orange-bellied parrot is considered endangered. Loss of coastal habitat for development and trapping for the aviculture trade are considered to be the primary causes of the species' past decline. Pressures for development on or adjacent to its main wintering areas and habitat alteration are now the main threats to its survival. A captive breeding program is now underway as part of a range of measures undertaken to ensure the future survival of the species.

Populations were modelled using the current carrying capacity (150), a reduced carrying capacity (50), and an increased carrying capacity (500). Simulations which involved varying mortality, capture, and supplementation rates of the wild population were run for all carrying capacities. Simulating the existing population using current data and management regimes indicated that the species would remain extant over the next 50 years at least, and stood a good chance of surviving for 100 years.

Reducing the carrying capacity to 50 under current conditions somewhat surprisingly did not increase the probability of extinction over 50 years, although genetic variability was greatly diminished. As would be expected, increasing the carrying capacity to 500 birds further reduced the prospects of extinction and greatly increased the genetic variability of the population. When modelled with an increased juvenile mortality rate (75% cf 50%), the population with the reduced carrying capacity showed a 70% probability of extinction within 50 years, while the current and increased carrying capacity populations showed extinction probabilities of 20% within that time. Imposing a capture and release captive breeding program on the populations only slightly decreased the extinction probability of the reduced carrying capacity, high mortality population, but greatly improved heterozygosity in the reduced carrying capacity, current mortality population. No extinctions occurred in the current and increased carrying capacity populations even at the high mortality levels, when simulated with supplementation from a captive breeding program. The simulations indicate several points. Juvenile mortality is of great significance to the health of the population. Any increase above the present rate of 50% greatly increases the probability of extinction, even with an enhanced habitat carrying capacity. The captive breeding program is an important back-up to the wild population, and will be extremely valuable if the wild population declines.

Evaluation of the Workshop

An evaluation was considered to be an important part of the workshop. All participants rated the background material supplied prior to the workshop as good to very good. Provision of background material was essential as very few participants had any prior experience with PVA. Organization was rated as very good to excellent by participants. The key to success was the large number of microcomputers available so that 2 to 3 people per computer was possible. Presentations were rated as very good to excellent.

The workshop format was considered to be a highly successful way of presenting PVA. PVA was considered to be a useful tool to aid threatened species management, providing its application and limitations were understood. PVA can focus attention on questions that should be addressed through additional research. PVA can be applied to well-studied taxa, and the general principles can be applied more widely to other taxa providing program characteristics are kept in perspective. All participants would recommend PVA as a management tool.

Conclusions

The PVA workshop proved a very useful way of quickly learning a new technique for threatened species management and conservation. PVA was applied to six species allowing a critical, quantitative analysis of extinction probabilities, as well as exploring management options to prevent species loss. PVA results will be used in forthcoming management plans and actions directed towards restoring these species to a status from which they will be relatively immune to extinction from random processes. In the future, it can be expected that PVA's will be carried out on additional endangered species to help manage their recovery.

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Essay

Assessing Extinction Threats: Toward a Reevaluation of IUCN Threatened Species Categories

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Abstract: *IUCN categories of threat (Endangered, Vulnerable, Rare, Indeterminate, and others) are widely used in 'Red lists' of endangered species and have become an important tool in conservation action at international, national, regional, and thematic levels. The existing definitions are largely subjective, and as a result, categorizations made by different authorities differ and may not accurately reflect actual extinction risks. We present proposals to redefine categories in terms of the probability of extinction within a specific time period, based on the theory of extinction times for single populations and on meaningful time scales for conservation action. Three categories are proposed (CRITICAL, ENDANGERED, VULNERABLE) with decreasing levels of threat over increasing time scales for species estimated to have at least a 10% probability of extinction within 100 years. The process of assigning species to categories may need to vary among different taxonomic groups, but we present some simple qualitative criteria based on population biology theory, which we suggest are appropriate at least for most large vertebrates. The process of assessing threat is clearly distinguished from that of setting priorities for conservation action, and only the former is discussed here.*

Resumen: *La categorización de la Unión Internacional para la Conservación de la Naturaleza (UICN) de las especies amenazadas (en peligro, vulnerables, raras, indeterminadas y otras) son ampliamente utilizadas en las Listas Rojas de especies en peligro y se han convertido en una herramienta importante para las acciones de conservación al nivel internacional, nacional, regional y temático. Las definiciones de las categorías existentes son muy subjetivas y, como resultado, las categorizaciones hechas por diferentes autores difieren y quizás no reflejen con certeza el riesgo real de extinción. Presentamos propuestas para re-definir las categorías en términos de la probabilidad de extinción dentro de un periodo de tiempo específico. Las propuestas están basadas en la teoría del tiempo de extinción para poblaciones individuales y en escalas de tiempo que tengan significado para las acciones de conservación. Se proponen tres categorías (CRITICA, EN PELIGRO, VULNERABLE) con niveles decrecientes de amenaza sobre escalas de tiempo en aumento para especies que se estima tengan cuando ménos un 10% de probabilidad de extinción en 100 años. El proceso de asignar especies a categorías puede que necesite variar dentro de los diferentes grupos taxonómicos pero nosotros presentamos algunos criterios cualitativos simples basados en la teoría de la biología de las poblaciones, las cuales sugerimos son apropiadas para cuando ménos la mayoría de los grandes vertebrados. El proceso de evaluar la amenaza se distingue claramente del de definir las prioridades para las acciones de conservación, sólamente el primero se discute aquí.*

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Introduction

Background

The Steering Committee of the Species Survival Commission (SSC) of the IUCN has initiated a review of the overall functioning of the Red Data Books. The review will cover three elements: (1) the form, format, content, and publication of Red Data Books; (2) the categories of threat used in Red Data Books and the IUCN Red List (Extinct, Endangered, Vulnerable, Rare, and Indeterminate); and (3) the system for assigning species to categories. This paper is concerned with the second element and includes proposals to improve the objectivity and scientific basis for the threatened species categories currently used in Red Data Books (see IUCN 1988 for current definitions).

There are at least three reasons why a review of the categorization system is now appropriate: (1) the existing system is somewhat circular in nature and excessively subjective. When practiced by a few people who are experienced with its use in a variety of contexts it can be a robust and workable system, but increasingly, different groups with particular regional or taxonomic interests are using the Red Data Book format to develop local or specific publications. Although this is generally of great benefit, the interpretation and use of the present threatened species categories are now diverging widely. This leads to disputes and uncertainties over particular species that are not easily resolved and that ultimately may negatively affect species conservation. (2) Increasingly, the categories of threat are being used in setting priorities for action, for example, through specialist group action plans (e.g., Oates 1986; Eudey 1988; East 1988, 1989; Schreiber et al. 1989). If the categories are to be used for planning then it is essential that the system used to establish the level of threat be consistent and clearly understood, which at present it does not seem to be. (3) A variety of recent developments in the study of population viability have resulted in techniques that can be helpful in assessing extinction risks.

Assessing Threats Versus Setting Priorities

In the first place it is important to distinguish systems for assessing threats of extinction from systems designed to help set priorities for action. The categories of threat should simply provide an assessment of the likelihood that if current circumstances prevail the species will go extinct within a given period of time. This should be a scientific assessment, which ideally should be completely objective. In contrast, a system for setting priorities for action will include the likelihood of extinction, but will also embrace numerous other factors, such as the likelihood that restorative action will be successful; economic, political, and logistical considerations; and perhaps the taxonomic distinctiveness of the species under review. Various categorization systems used in the past, and proposed more recently, have confounded these two processes (see Fitter & Fitter 1987; Munton 1987). To devise a general system for setting priorities is not useful because different concerns predominate within different taxonomic, ecological, geographical, and political units. The process of setting priorities is therefore best left to specific plans developed by specialist bodies such as the national and international agencies, the specialist groups, and other regional bodies that can devise priority assessments in the appropriate regional or taxonomic context. An objective assessment of extinction risk may also then contribute to the decisions taken by governments on which among a variety of recommendations to implement. The present paper is therefore confined to a discussion of assessing threats.

Aims of the System of Categorization

For Whom?

Holt (1987) identifies three different groups whose needs from Red Data Books (and therefore categories of threat) may not be mutually compatible: the lay public, national and international legislators, and conservation professionals. In each case the purpose is to highlight taxa with a high extinction risk, but there are differences in the quality and quantity of information needed to support the assessment. Scott et al. (1987) make the point that in many cases simple inclusion in a Red Data Book has had as much effect on raising awareness as any of the supporting data (see also Fitter 1974). Legislators need a simple, but objective and soundly based system because this is most easily incorporated into legislation (Bean 1987). Legislators frequently require some statement about status for every case they consider, however weak the available information might be. Inevitably, therefore, there is a conflict between expediency and the desire for scientific credibility and objectivity. Conservationists generally require more precision, particularly if they are involved in planning conservation programs that aim to make maximal use of limited resources.

Characteristics of an Ideal System

With this multiplicity of purposes in mind it is appropriate to consider various characteristics of an ideal system:

(1) The system should be essentially simple, providing easily assimilated data on the risk of extinction. In terms of assessing risk, there seems to be little virtue in developing numerous categories, or in categorizing risk on the basis of a range of different parameters (e.g., abundance, nature of threat, likelihood of persistence of threat, etc.). The categories should be few in number,

should have a clear relationship to one another (Holt 1987; Munton 1987), and should be based around a probabilistic assessment of extinction risk.

(2) The system for categorization has to be flexible in terms of data required. The nature and amount of data available to assess extinction risks varies widely from almost none (in the vast majority of species) to highly detailed population data (in a very few cases). The categorization system should make maximum use of whatever data are available. One beneficial consequence of this process would be to identify key population data for field workers to collect that would be useful in assessing extinction risk.

(3) The categorization system also needs to be flexible in terms of the population unit to which it applies. Throughout this discussion, it is assumed that the system being developed will apply to any species, subspecies, or geographically separate population. The categorization system therefore needs to be equally applicable to limited lower taxonomic levels and to more limited geographical scope. Action planning will need to be focused on particular taxonomic groups or geographical areas, and can then incorporate an additional system for setting priorities that reflect taxonomic distinctiveness and extinction risks outside the local area (e.g., see East 1988, 1989; Schreiber et al. 1989).

(4) The terminology used in categorization should be appropriate, and the various terms used should have a clear relationship to each other. For example, among the current terms both 'endangered' and 'vulnerable' are readily comprehended, but 'rare' is confusing. It can be interpreted as a statement about distribution status, level of threat, or local population size, and the relationships between these factors are complex (Rabinowitz et al. 1986). Rare (i.e., low-density) species are not always at risk and many species at risk are not numerically rare (King 1987; Munton 1987; Heywood 1988). The relationship of 'rare' to 'endangered' and 'vulnerable' is also unclear.

(5) If the system is to be objectively based upon sound scientific principles, it should include some assessment of uncertainty. This might be in terms of confidence levels, sensitivity analyses, or, most simply, on an ordinal scale reflecting the adequacy of the data and models in any particular case.

(6) The categories should incorporate a time scale. On a geological time scale all species are doomed to extinction, so terms such as "in danger of extinction" are rather meaningless. The concern we are addressing here is the high background level of the current rates of extinction, and one aim is therefore preservation over the upcoming centuries (Soulé & Simberloff 1986). Therefore, the probability of extinction should be expressed in terms of a finite time scale, for example, 100 years. Munton (1987) suggests using a measure of number of years until extinction. However, since most models of population extinction times result in approximately exponential distributions, as in Goodman's (1987) model of density-dependent population growth in a fluctuating environment, mean extinction time may not accurately reflect the high probability that the species will go extinct within a time period considerably shorter than the mean (see Fig. 1). More useful are measures such as "95% likelihood of persistence for 100 years."

Population Viability Analysis and Extinction Factors

Various approaches to defining viable populations have been taken recently (Shaffer 1981, 1990; Gilpin & Soulé, 1986; Soulé 1987). These have emphasized that there is no simple solution to the question of what constitutes a viable population. Rather, through an analysis of extinction factors and their interactions it is possible to assess probabilities and time scales for population persistence for a particular taxon at a particular time and place. The development of population viability analyses has led to the definition of intrinsic and extrinsic factors that determine extinction risks (see Soulé 1983; Soulé 1987; Gilpin & Soulé 1986; see also King 1987). Briefly these can be summarized as population dynamics (number of individuals, life history and age or stage distribution, geographic structure, growth rate, variation in demographic parameters), population characteristics (morphology, physiology, genetic variation, behavior and dispersal patterns), and environmental effects (habitat quality and quantity, patterns and rates of environmental disturbance and change, interactions with other species including man).

Preliminary models are available to assess a population's expected persistence under various extinction pressures, for example, demographic variation (Goodman 1987*a*, *b*; Belovsky 1987; CBSG 1989), catastrophes (Shaffer 1987), inbreeding and loss of genetic diversity (Lande & Barrowclough 1987; Lacy 1987), metapopulation structure (Gilpin 1987; Quinn & Hastings 1987; Murphy et al. 1990). In addition, various approaches have been made to modeling extinction in populations threatened by habitat loss (e.g., Gutiérrez & Carey 1985; Maguire et al. 1987; Lande 1988), disease (e.g., Anderson & May 1979; Dobson & May 1986; Seal et al. 1989), parasites (e.g., May & Anderson 1979; May & Robinson 1985; Dobson & May 1986), competitors, poaching (e.g., Caughley 1988), and harvesting or hunting (e.g., Holt 1987).

So far, the development of these models has been rather limited, and in particular they often fail to successfully incorporate several different extinction factors and their interactions (Lande 1988). Nevertheless the approach has been applied in particular cases even with

existing models (e.g., grizzly bear: Shaffer 1983; spotted owl: Gutiérrez & Carey 1985; Florida panther: CBSG 1989), and there is much potential for further development.

Although different extinction factors may be critical for different species, other, noncritical factors cannot be ignored. For example, it seems likely that for many species, habitat loss constitutes the most immediate threat. However, simply preserving habitats may not be sufficient to permit long term persistence if surviving populations are small and subdivided and therefore have a high probability of extinction from demographic or genetic causes. Extinction factors may also have cumulative or synergistic effects; for example, the hunting of a species may not have been a problem before the population was fragmented by habitat loss. In every case, therefore, all the various extinction factors and their interactions need to be considered. To this end more attention needs to be directed toward development of models that reflect the random influences that are significant to most populations, that incorporate the effects of many different factors, and that relate to the many plant, invertebrate, and lower vertebrate species whose population biology has only rarely been considered so far by these methods.

Viability analysis should suggest the appropriate kind of data for assigning extinction risks to species, though much additional effort will be needed to develop appropriate models and collect appropriate field data.

Proposal

Three Categories and Their Justification

We propose the recognition of three categories of threat (plus EXTINCT), defined as follows:

CRITICAL:	50% probability of extinction within 5 years or 2 generations, whichever is longer.
ENDANGERED:	20% probability of extinction within 20 years or 10 generations, whichever is longer.
VULNERABLE:	10% probability of extinction within 100 years.

These definitions are based on a consideration of the theory of extinction times for single populations as well as on meaningful time scales for conservation action. If biological diversity is to be maintained for the foreseeable future at anywhere near recent levels occurring in natural ecosystems, fairly stringent criteria must be adopted for the lowest level of extinction risk, which we call VULNERABLE. A 10% probability of extinction within 100 years has been suggested as the highest level of risk that is biologically acceptable (Shaffer 1981) and seems appropriate for this category. Furthermore, events more than about 100 years in the future are hard to foresee, and this may be the longest duration that legislative systems are capable of dealing with effectively.

It seems desirable to establish a CRITICAL category to emphasize that some species or populations have a very high risk of extinction in the immediate future. We propose that this category include species or populations with a 50% chance of extinction within 5 years or two generations, and which are clearly at very high risk.

An intermediate category, ENDANGERED, seems desirable to focus attention on species or populations that are in substantial danger of extinction within our lifetimes. A 20% chance of extinction within 20 years or 10 generations seems to be appropriate in this context.

For increasing levels of risk represented by the categories VULNERABLE, ENDANGERED, and CRITICAL, it is necessary to increase the probability of extinction or to decrease the time scale, or both. We have chosen to do both for the following reasons. First, as already mentioned, decreasing the time scale emphasizes the immediacy of the situation. Ideally, the time scale should be expressed in natural biological units of generation time of the species or population (Leslie 1966), but there is also a natural time scale for human activities such as conservation efforts, so we have given time scales in years and in generations for the CRITICAL and ENDANGERED categories.

Second, the uncertainty of estimates of extinction probabilities decreases with increasing risk levels. In population models incorporating fluctuating environments and catastrophes, the probability distribution of extinction times is approximately exponential (Nobile et al. 1985; Goodman 1987). In a fluctuating environment where a population can become extinct only through a series of unfavorable events, there is an initial, relatively brief period in which the chance of extinction is near zero, as in the inverse Gaussian distribution of extinction times for density-independent fluctuations (Ginzburg et al. 1982; Lande & Orzack 1988). If catastrophes that can extinguish the population occur with probability p per unit time, and are much more important than normal environmental fluctuations, the probability distribution of extinction times is approximately exponential, pe^{-pt}, and the cumulative probability of extinction up to time t is approximately $1 - e^{-pt}$. Thus, typical probability distributions of extinction times look like the curves in Figures 1A and 1B, and the cumulative probabilities of extinction up to any given time look like the curves in Figures 1C and 1D. Dashed curves represent different distributions of extinction times and cumulative extinction probabilities obtained by changing the model parameters in a formal population viability analysis (e.g., different amounts of environmental variation in demographic parameters). The uncertainty in an

estimate of cumulative extinction probability up to a certain time can be measured by its coefficient of variation, that is, the standard deviation among different estimates of the cumulative extinction probability with respect to reasonable variation in model parameters, divided by the best estimate. It is apparent from Figures 1C and 1D that at least for small variations in the parameters (if the parameters are reasonably well known), the uncertainty of estimates of cumulative extinction probability at particular times decreases as the level of risk increases. Thus at times, t_1, t_2, and t_3 when the best estimates of the cumulative extinction probabilities are 10%, 20%, and 50% respectively, the corresponding ranges of extinction probabilities in Figure 1C are 6.5%–14.8%, 13.2%–28.6%, and 35.1%–65.0%, and in Figure 1D are 6.8%–13.1%, 13.9%–25.7%, and 37.2%–60.2%. Taking half the range as a rough approximation of the standard deviation in this simple illustration gives uncertainty measures of 0.41, 0.38, and 0.30 in Figure 1C, and 0.31, 0.29, and 0.23 in Figure 1D, corresponding to the three levels of risk. Given that for practical reasons we have chosen to shorten the time scales for the more threatened categories, these results suggest that to maintain low levels of uncertainty, we should also increase the probabilities of extinction in the definition of the ENDANGERED and CRITICAL categories.

These definitions are based on general principles of population biology with broad applicability, and we believe them to be appropriate across a wide range of life forms. Although we expect the process of assigning species to categories (see below) to be an evolving (though closely controlled and monitored) process, and one that might vary across broad taxonomic groups, we recommend that the definitions be constant both across taxonomic groups and over time.

Assigning Species or Populations to Categories

We recognize that in most cases, there are insufficient data and imperfect models on which to base a formal probabilistic analysis. Even when considerable information does exist there may be substantial uncertainties in the extinction risks obtained from population models containing many parameters that are difficult to estimate accurately. Parameters such as environmental stochasticity (temporal fluctuations in demographic parameters such as age- or developmental stage–specific mortality and fertility rates), rare catastrophic events, as well as inbreeding depression and genetic variability in particular characters required for adaptation are all difficult to estimate accurately. Therefore it may not be possible to do an accurate probabilistic viability analysis even for some very well studied species. We suggest that the categorization of many species should be based on more qualitative criteria derived from the same body of theory as the definitions above, which will broaden the scope and applicability of the categorization system. In these more qualitative criteria we use measures of effective population size (N_e) and give approximate equivalents in actual population size (N). It is important to recognize that the relationship between N_e and N depends upon a variety of interacting factors. Estimating N_e for a particular population will require quite extensive information on breeding structure and life history characteristics of the population and may then produce only an approximate figure (Lande & Barrowclough 1987). In addition, different methods of estimating N_e will give variable results (Harris & Allendorf 1989). N_e/N ratios vary widely across species, but are typically in the range 0.2 to 0.5. In the criteria below we give a value for N_e as well as an approximate value of N assuming that the N_e/N ratio is 0.2.

We suggest the following criteria for the three categories:

CRITICAL: 50% probability of extinction within 5 years or 2 generations, whichever is longer, or

(1) Any two of the following criteria:
- (a) Total population $N_e < 50$ (corresponding to actual $N < 250$).
- (b) Population fragmented: ≤2 subpopulations with $N_e > 25$ ($N > 125$) with immigration rates <1 per generation.
- (c) Census data of >20% annual decline in numbers over the past 2 years, or >50% decline in the last generation, or equivalent projected declines based on demographic projections after allowing for known cycles.
- (d) Population subject to catastrophic crashes (>50% reduction) per 5 to 10 years, or 2 to 4 generations, with subpopulations highly correlated in their fluctuations.

or (2) Observed, inferred, or projected habitat alteration (i.e., degradation, loss, or fragmentation) resulting in characteristics of (1).

or (3) Observed, inferred, or projected commercial exploitation or ecological interactions with introduced species (predators, competitors, pathogens, or parasites) resulting in characteristics of (1).

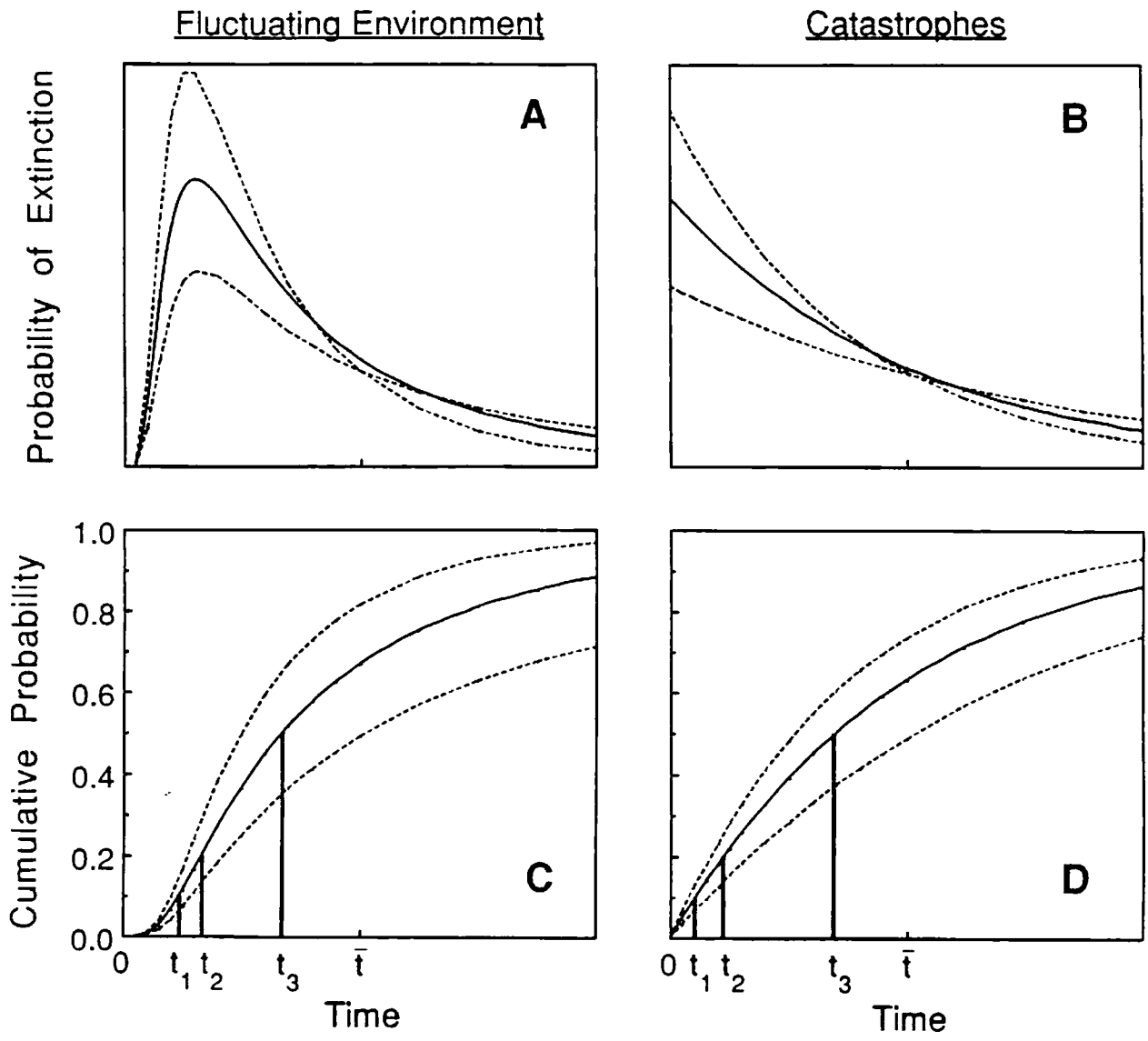

Figure 1. Probability distributions of time to extinction in a fluctuating environment, inverse Gaussian distributions (A), or with catastrophes, exponential distributions (B). Corresponding cumulative extinction probabilities of extinction up to any given time are shown below (C and D). Solid curves represent the best estimates from available data and dashed curves represent different estimates based upon the likely range of variation in the parameters. t_1, t_2, and t_3 are times at which the best estimates of cumulative extinction probabilities are 10%, 20%, and 50%. $\bar{t}$ is the expected time to extinction in the solid curves.

ENDANGERED:

20% probability of extinction within 20 years or 10 generations, whichever is longer, or

(1) Any **two** of the following or any **one** criterion under CRITICAL

(a) Total population $N_e < 500$ (corresponding to actual $N < 2,500$).

(b) Population fragmented:
(i) ≤ 5 subpopulations with $N_e > 100$ ($N > 500$) with immigration rates <1 per generation, or
(ii) ≤ 2 subpopulations with $N_e > 250$ ($N > 1,250$) with immigration rates <1 per generation.

(c) Census data of $>5\%$ annual decline in numbers over past 5 years, or $>10\%$ decline per generation over past 2 generations, or equivalent projected declines based on demographic data after

allowing for known cycles.

(d) Population subject to catastrophic crashes: an average of >20% reduction per 5 to 10 years or 2 to 4 generations, or >50% reduction per 10 to 20 years or 5 to 10 generations, with subpopulations strongly correlated in their fluctuations.

or (2) Observed, inferred, or projected habitat alteration (i.e., degradation, loss, or fragmentation) resulting in characteristics of (1).

or (3) Observed, inferred, or projected commercial exploitation or ecological interactions with introduced species (predators, competitors, pathogens, or parasites) resulting in characteristics of (1).

VULNERABLE:

10% probability of extinction within 100 years, or

(1) Any **two** of the following criteria or any **one** criterion under ENDANGERED.

(a) Total population N_e < 2,000 (corresponding to actual N < 10,000).

(b) Population fragmented:
(i) ≤5 subpopulations with N_e > 500 (N > 2,500) with immigration rates <1 per generation, or
(ii) ≤2 subpopulations with N_e > 1,000 (N > 5,000) with immigration rates <1 per generation.

(c) Census data of >1% annual decline in numbers over past 10 years, or equivalent projected declines based on demographic data after allowing for known cycles.

(d) Population subject to catastrophic crashes: an average of >10% reduction per 5 to 10 years, >20% reduction per 10 to 20 years, or >50% reduction per 50 years, with subpopulations strongly correlated in their fluctuations.

or (2) Observed, inferred, or projected habitat alteration (i.e., degradation, loss, or fragmentation) resulting in characteristics of (1).

or (3) Observed, inferred, or projected commercial exploitation or ecological interactions with introduced species (predators, competitors, pathogens, or parasites) resulting in characteristics of (1).

Prior to any general acceptance, we recommend that these criteria be assessed by comparison of the categorizations they lead to in particular cases with the results of formal viability analyses, and categorizations based on existing methods. This process should help to resolve uncertainties about both the practice of, and results from, our proposals. We expect a system such as this to be relatively robust and of widespread applicability, at the very least for most higher vertebrates. For some invertebrate and plant taxa, different kinds of criteria will need to be developed within the framework of the definitions above. For example, many of these species have very high rates of population growth, short generation times, marked or episodic fluctuations in population size, and high habitat specificity. Under these circumstances, it will be more important to incorporate metapopulation characteristics such as subpopulation persistence times, colonization rates, and the distribution and persistence of suitable habitats into the analysis, which are less significant for most large vertebrate populations (Murphy et al. 1990; Menges 1990).

Change of Status

The status of a population or species with respect to risk of extinction should be up-listed (from unlisted to VULNERABLE, from VULNERABLE to ENDANGERED, or from ENDANGERED to CRITICAL) as soon as current information suggests that the criteria are met. The status of a population or species with respect to risk of extinction should be down-listed (from CRITICAL to ENDANGERED, from ENDANGERED to VULNERABLE, or from VULNERABLE to unlisted) only when the criteria of the lower risk category have been satisfied for a time period equal to that spent in the original category, or if it is shown that past data were inaccurate.

For example, if an isolated population is discovered consisting of 500 individuals and no other information is available on its demography, ecology, or the history of the population or its habitat, this population would initially be classified as ENDANGERED. If management efforts, natural events, or both caused the population to increase so that 10 years later it satisfied the criteria of the VULNERABLE category, the population would not be removed from the ENDANGERED category for a further period of 10 years. This time lag in down-listing prevents frequent up-listing and down-listing of a population or species.

Uncertain or Conflicting Results

Because of uncertainties in parameter estimates, especially those dealing with genetics and environmental

variability and catastrophes, substantial differences may arise in the results from analyses of equal validity performed by different parties. In such cases, we recommend that the criteria for categorizing a species or population should revert to the more qualitative ones outlined above.

Reporting Categories of Threat

To objectively compare categorizations made by different investigators and at different times, we recommend that any published categorization also cite the method used, the source of the data, a date when the data were accurate, and the name of the investigator who made the categorization. If the method was by a formal viability model, then the name and version of the model used should also be included.

Conclusion

Any system of categorizing degrees of threat of extinction inevitably contains arbitrary elements. No single system can adequately cover every possibility for all species. The system we describe here has the advantage of being based on general principles from population biology and can be used to categorize species for which either very little or a great deal of information is available. Although this system may be improved in the future, we feel that its use will help to promote a more uniform recognition of species and populations at risk of premature extinction, and should thereby aid in setting priorities for conservation efforts.

Summary

1. Threatened species categories should highlight species vulnerable to extinction and focus appropriate reaction. They should therefore aim to provide objective, scientifically based assessments of extinction risks.
2. The audience for Red Data Books is diverse. Positive steps to raise public awareness and implement national and international legislation benefit from simple but soundly based categorization systems. More precise information is needed for planning by conservation bodies.
3. An ideal system needs to be simple but flexible in terms of data required. The category definitions should be based on a probabilistic assessment of extinction risk over a specified time interval, including an estimate of error.
4. Definitions of categories are appropriately based on extinction probabilities such as those arising from population viability analysis methods.
5. We recommend three categories, CRITICAL, ENDANGERED, and VULNERABLE, with decreasing probabilities of extinction risk over increasing time periods.
6. For most cases, we recommend development of more qualitative criteria for allocation to categories based on basic principles of population biology. We present some criteria that we believe to be appropriate for many taxa, but are appropriate at least for higher vertebrates.

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Loss of Genetic Diversity from Managed Populations: Interacting Effects of Drift, Mutation, Immigration, Selection, and Population Subdivision

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Abstract: *A computer simulation program was used to examine interacting effects of genetic drift, mutation, immigration from outside populations, directional and balancing selection, and population subdivision on the loss of genetic variability from small, managed populations. Stochastic events were simulated with a pseudo-random number generator, and the genetic variation (expected heterozygosity) within and between populations was monitored in 25 populations for 100 generations.*

Genetic drift was the overriding factor controling the loss of genetic variation. Mutation has no noticeable effect on populations of the size typically managed in zoos and nature preserves. Immigration from a large source population can strikingly slow, halt, or even reverse the loss of genetic variation, even with only one or a few migrants per generation. Unless selection is stronger than commonly observed in natural populations, it is inefficient in countering drift when population sizes are on the order of 100 or fewer. Subdivided populations rapidly lose variability from within each subpopulation but retain variation across the subpopulations better than does a panmictic population.

These results suggest that population managers should be concerned with the variation-depleting effects of genetic drift, perhaps almost to the exclusion of consideration of selection and mutation. Drift can be countered by the introduction of very occasional immigrants or, less effectively, by division of the managed population into smaller breeding groups that interchange enough migrants to prevent unacceptably deleterious inbreeding within each subpopulation.

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Resumen: *A través de un programa de simulación por computadora se examinaron los efectos interactivos de la deriva génica, las mutaciones, la inmigración de poblaciones externas, la selección balanceada y direccional, y la subdivisión de poblaciones pequeñas sujetas a manejo, debido a la pérdida de variabilidad genética. Se simularon eventos estocásticos con un generador de números pseudo-azarosos y se estudió la variación genética intra e interpoblacional (heterocigosis esperada) en 25 poblaciones durante 100 generaciones.*

La deriva génica fue el factor predominante que controló la pérdida de variación genética. Las mutaciones no tuvieron un efecto notable en poblaciones del tamaño típico manejado en zoológicos y áreas protegidas. La inmigración proveniente de otras poblaciones más grandes puede asombrosamente disminuir, detener ó invertir la pérdida de variación genética, aún con la influencia de sólo uno o pocos migrantes por generación. Cuando el tamaño de las poblaciones es del orden de 100 individuos ó menos, no es necesario evaluar la deriva génica, a menos que la selección sea más fuerte que la comunmente observada en poblaciones naturales. Las poblaciones divididas pierden rápidamente su variabilidad intra- subpoblacional, pero retienen una mayor variación intersubpoblacional que las poblaciones panmíticas.

Los resultados sugieren que los manejadores de poblaciones deben estar más atentos a la disminución de la variación genética producida por la deriva génica, que a las mutaciones ó a la selección natural. La deriva génica puede invertirse con la introducción de migrantes ocasionales, ó (aunque menos efectivamente) a través de la división de las poblaciones manejadas en pequeños grupos de crianza que puedan intercambiar migrantes para prevenir cruzamientos deletéreos dentro de cada subpoblación.

Introduction

As natural habitats disappear and populations of organisms within remaining natural areas are increasingly exploited, many species are reduced to small, remnant populations occupying what is left of the habitat. Populations being propagated in zoos and intensively managed wildlife parks represent an extreme in these respects, at times being the last hope for survival of a species. By virtue of careful management, captive populations can be largely freed from the hazards of predation, inadequate nutrition, severe weather, disease, and difficulty in finding mates. Thus, smaller and more stable populations can be maintained in zoos or closely managed nature preserves than would persist in more natural environments.

Yet small populations of organisms lose genetic diversity over time. In the absence of any deterministic or directional forces on gene frequencies (selection, migration, mutation), frequencies of alleles follow a random walk process ("genetic drift") due to the random sampling of genes during transmission from one generation to the next. The random sampling of a small number of genes at each new generation results in greater fluctuations in gene frequencies than does the sampling of a larger number of genes. Therefore, small populations will tend to lose genetic variation by genetic drift more rapidly than will larger populations. The ultimate fate of any sexual population lacking mechanisms to restore genetic variation would be fixation of one allele at each genetic locus throughout the genome.

An immediate effect of the depletion of genetic variability is increasing homozygosity of the individuals in the population. Although the causes are still debated (Crow 1948, Lerner 1954, Clarke 1979, Frankel 1983), it has been widely recognized that increases in homozygosity often lead to lower viability and fecundity ("inbreeding depression") (Falconer 1981, Ralls & Ballou 1983).

Over a longer time scale, although the harmful effects of inbreeding on individuals may diminish as deleterious recessive genes are removed from the population by selection (Lynch 1977, Templeton & Read 1983), the population as a whole loses the evolutionary flexibility conferred by genetic diversity (Sèlander 1983). Without genetic variation between individuals on which natural selection can act, a population cannot adapt to changing environments and is vulnerable to new predators, diseases, parasites, climatic conditions, and competitors, and to changing food supplies.

For captive populations the loss of evolutionary flexibility may be especially rapid and particularly hazardous to long-term survival. The combined effect of rapid genetic drift in small captive populations and strong directional selection for survival in a novel captive environment might quickly deplete genetic variation. The relative lack of predators and abundance of food and shelter might lead to a relaxation of many selective pressures to which wild populations would be exposed. Yet the restoration of genetic variation by mutation following this relaxation of selection for traits formerly under stringent selection is a very slow process—probably too slow to be of consequence in current efforts toward the preservation of species. For a given genetic locus, only one new mutation per thousand generations would be expected in a typical captive population of 100 to 1000 individuals. The rapid rate of habitat alteration is not likely to slow, so the species harbored by zoos will need considerable adaptive flexibility (evolutionary, physiological, and behavioral) if they are ever again to thrive in a noncaptive setting.

If zoos (or wildlife preserves and parks) are to propagate long-term viable populations, and especially if they are to contribute to the preservation of species diversity, they will have to manage their populations in such a way as to minimize, halt, or even reverse the decline in genetic variability that occurs in captive populations. Large breeding populations, exposed to varied environments, will maintain genetic variation and evolutionary flexibility better than will smaller populations in less varied habitats (Levins 1968, Hedrick et al. 1976, Lacy 1982). With finite resources, however, allocation of space and facilities for one species necessarily limits space allocated to others. Efforts are needed to determine how best to manage captive breeding populations so as to make optimal use of those resources set aside for each species.

One approach to understanding how varied evolutionary forces effect genetic variation in small populations, and how populations can be managed to make those forces work toward the goals of captive management instead of against them, is to use computers to simulate the complex interactions of factors impinging on hypothetical populations. Computer models share with analytical theoretical approaches the property that results are dependent upon necessarily incomplete representations of natural processes. Models may be sensitive to incorrect assumptions, and important factors may have been omitted. Yet, for studying the effects of variables that can be well-defined, and for examining interactions among those variables, computer simulations can provide answers that may not be intuitive and that may not be readily obtainable by mathematical analysis. Moreover, many of the analytical models in the literature and many of the intuitive concepts about genetic diversity in small populations have been inadequately if at all examined by simulations. Unlike many analytical models, computer simulations do not make approximations that depend on the range of parameters for accuracy. The order-of-magnitude approximations of many analytical treatments are often not sufficiently informative for population managers.

In this paper I describe a general computer simulation model used to examine the effects of population size, mutation, immigration, selection, and population subdivision, and their interactions, on the maintenance of genetic variability in small, managed populations. Many of these factors have been examined before, either analytically or by simulation models, but the disparity among the models used to examine these factors makes comparisons of the effects, and of the resulting recommendations, difficult. Finally, because models are built on simplifying assumptions, the robustness of the conclusions derived from any model (including those presented here) should be verified by alternative approaches before they are put into practice.

Methods

A computer simulation program was written in the C programming language for use on microcomputers using the MS-DOS (Microsoft, Inc.) operating system. Results were output numerically via a printer and graphically via a Hewlett-Packard 7475A plotter.

To simulate the fate of two alleles at a genetic locus, the program

1. Prompts the user to input the number of populations to be simulated, number of generations, population size, genotype fitnesses, forward and backward mutation rates, frequency of immigration into the population from an outside population, number of subpopulations into which the total population is fragmented, and migration rate between subdivisions.
2. Creates a population (composed of several subpopulations, if specified in step 1) of diploid individuals, assigning two alleles to each individual with probability 0.5 that each allele is of one type (say, "A") rather than the other ("a"). (Probabilistic events in the simulation are determined to occur when a real number drawn at random from a uniform distribution from 0 to 1 is less than the specified probability.)
3. Selects two parents at random from each (sub)population. Each parent is used for that mating with a probability equal to the fitness assigned to its genotype relative to the fitness of the most fit genotype. If a parent is not used, a replacement is drawn at random from the (sub)population, and then that newly chosen parent is in turn kept or discarded with probability determined by its relative fitness.
4. Randomly selects one allele from each of the two parents and assigns that allele pair to an offspring.
5. Replaces the offspring with a migrant from another subpopulation, with probability equal to the migration rate between subpopulations. The migrant has a genotype that is drawn at random from the pool of genotypes present in the other subpopulations.
6. Replaces the individual with an immigrant from an outside population, with probability equal to the specified outside immigration rate. The immigrant has a genotype randomly drawn from a gene pool in which the two allelic variants are equally frequent (as in the starting population).
7. Allows each of the two alleles of the individual to mutate to their respective alternate form, with probabilities equal to the specified mutation rate.
8. Repeats steps 3 through 7 (for each subpopulation) as often as is necessary to create a new generation of the specified size.
9. Calculates allele frequencies and percent "expected" heterozygosity within each subpopulation, that is, the heterozygosity that would be observed if the subpopulation were in perfect Hardy-Weinberg equilibrium. The expected heterozygosity (calculated as $2pq$, in which p and q are the frequencies of the two alleles) is twice the binomial variance in allelic frequencies in the population (Crow & Kimura 1970). The program also calculates allele frequencies averaged over subpopulations and from these overall allele frequencies calculates the "total heterozygosity" or "gene diversity" that would be present in the population if it were in Hardy-Weinberg equilibrium (mating at random with no subdivision) (Nei 1973,1977). The total heterozygosity reflects both within-subpopulation heterozygosity and any between-subpopulation genetic differentiation. If all subpopulations are genetically alike, then the total heterozygosity will be equal to the (also equal) heterozygosities of the subpopulations. If subpopulations are genetically quite distinct, then the total heterozygosity will be much larger than is the average within-subpopulation heterozygosity, and it is the heterozygosity that would be present in a single randomly breeding population with the same amount of genetic diversity (strictly, the same total variance in alleles) as is present across the subpopulations.
10. Repeats steps 3 through 9 for the specified number of generations, beginning each generation with the offspring from the previous generation.

Thus, the program simulates genetic processes in a constant size, randomly breeding population of sexually reproducing hermaphrodites with discrete generations. An individual can mate with itself, but is no more likely to do so than to mate with any other given individual. One important way in which the modeled population deviates from reality is the randomness of breeding within

the (sub)populations. In almost any real population, mate selection, polygamy, and sex-biased dispersal and mortality lead to deviations from panmixia. If these factors can be estimated for a population under study, then the "effective population size" can be calculated and a conversion made between the real population and the ideal populations presented in generalized models such as this. The effective size of a population is the size of an idealized monoecious population with random union of gametes, that would lose heterozygosity at the same rate as the observed population (Wright 1969). Thus, in the simulated (sub)populations, the actual population size is also the effective population size.

The lack of separate sexes and the self-compatibility are atypical of most captive populations, but the genetic behavior of such a population is almost indistinguishable from that of a population with separate sexes. A few simulations were run with the constraint that an individual could not mate with itself, and the results did not differ from simulations without such a constraint. Excluding self-fertilization has the same effect as consideration of separate sexes; either increases the genetically effective population size by 0.5 individuals (Wright 1969). The exclusion of sib-mating, as is commonly observed in wild populations (Ralls et al. 1986) and is often an intent of captive breeding programs, results in an effective population of just two greater than the idealized population modeled here (Wright 1969). An unequal sex ratio or nonrandom mating (producing a variance in family sizes that is greater than Poisson) can reduce the effective size to a fraction of the total population size (Crow & Kimura 1970, Ryman et al. 1981). In captive populations, these causes of low effective population size can be minimized (Flesness 1977, Denniston 1978). In fact, if family sizes are equalized, effective population approaches twice the real population size (Crow & Kimura 1970).

I monitored genetic diversity in the simulations using expected heterozygosities, both average within-subpopulation heterozygosity and the total (within- and between-subpopulation) heterozygosity that would be observed if all subpopulations were mixed at random and the genotypes were in Hardy-Weinberg proportions. Genetic diversity could have been expressed as the number of alleles present ("allelic diversity"), as in the simulations of Allendorf (1986) and the analytical models of Fuerst and Maruyama (1986). For several reasons heterozygosity is the more common measure of genetic diversity, but both measures yield important insights. Being proportional to genetic variance, the expected heterozygosity is also proportional to the short-term response to selection on that genetic locus (Fisher's Fundamental Theorem of Natural Selection: Fisher 1958). Long-term response to selection, however, is more dependent upon the alleles present in the population than on initial frequencies or heterozygosity (Allendorf 1986). Unlike allelic diversity, the estimation of expected heterozygosity from a sample of a population is not highly dependent upon the sample size observed. Also, the fate of allelic diversity in a population is quite dependent upon the starting conditions (numbers and frequencies of alleles: Allendorf 1986), whereas heterozygosity decays at a steady average rate regardless of the initial allele frequencies in the population (Crow & Kimura 1970).

Results

Figure 1 shows the fate of heterozygosity in 25 simulated populations of 120 individuals across 100 generations. (A population size of 120 will be used frequently in this paper as a standard of comparison.) The only force leading to changes in gene frequencies and heterozygosities in Figure 1 is random genetic drift. All genotypes were assigned the same fitness, there was no mutation or immigration, and mating was random.

The stochastic nature of genetic transmission is apparent in the simulated populations, even though the populations are not unrealistically small for captive or even wild populations of large vertebrates. Three of the 25 populations lost all heterozygosity at the genetic locus within 100 generations (i.e., one of the two allelic variants was lost, the other was fixed), and yet six populations had virtually the same allele frequencies and heterozygosities after 100 generations as they had at the outset. The average heterozygosity in these 25 simulated populations after 100 generations was 58.25 percent of the initial value (SE = 7.19%), not significantly different from the 66 percent predicted from the commonly used equation for the loss of heterozygosity by random drift

$$H_t = (1 - 1/[2N_e])^t H_0$$

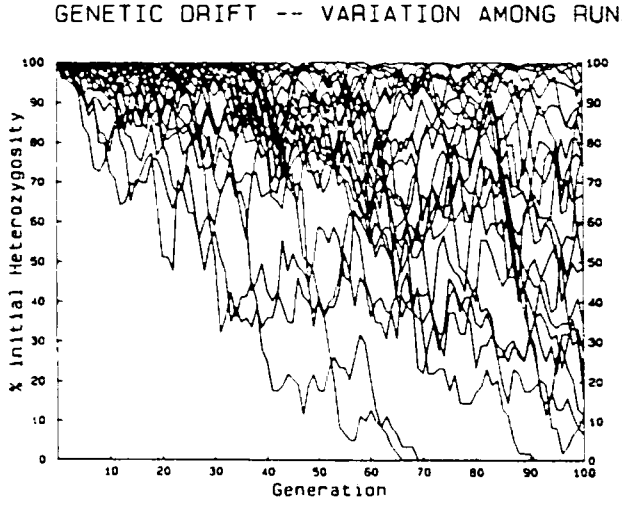

Figure 1. Percent heterozygosity retained across 100 generations in 25 simulated populations of 120 randomly mating individuals each.

in which N_e is the effective population size, and H_0 and H_t are heterozygosities at generations 0 and t, respectively.

Throughout the remainder of this paper, heterozygosities averaged across 25 simulated populations will be shown for each set of conditions discussed. The average behavior of the 25 simulations can represent the fate of a given genetic locus across 25 populations, or the fate of 25 genetic loci within one population. The relative smoothness of average heterozygosities shown in all subsequent figures should not obscure the fact that underlying the average heterozygosities are fates of individual populations that are as diverse as those shown in Figure 1. Results revealed by simulations are thus the "expected" behavior of a population only in a statistical sense: They should not be used to predict the behavior of a particular gene of interest. For example, only a few populations in Figure 1 were left with fractions of the initial heterozygosity close to the theoretical prediction of 66 percent.

Effect of Population Size

Figure 2 compares average heterozygosities of 25 simulated populations of various sizes and shows the effect of population size on the rate at which genetic drift depletes variation. Mean heterozygosities after 100 generations did not vary significantly from the theoretical values of 90.5 percent, 81.2 percent, 65.9 percent, 43.3 percent, 28.4 percent, and 8.0 percent that are expected for populations of size 500, 240, 120, 60, 40, and 20, respectively. Standard errors of the mean heterozygosities across these 25 simulated populations of each size (SE = 2.73%, 4.58%, 6.86%, 7.75%, 8.48%, and 2.79%, respectively) approximate the theoretical standard errors for heterozygosities remaining after 100 generations of drift (2.43%, 4.35%, 6.60%, 8.00%, 7.66%, and 4.79%; equation from Bulmer 1985).

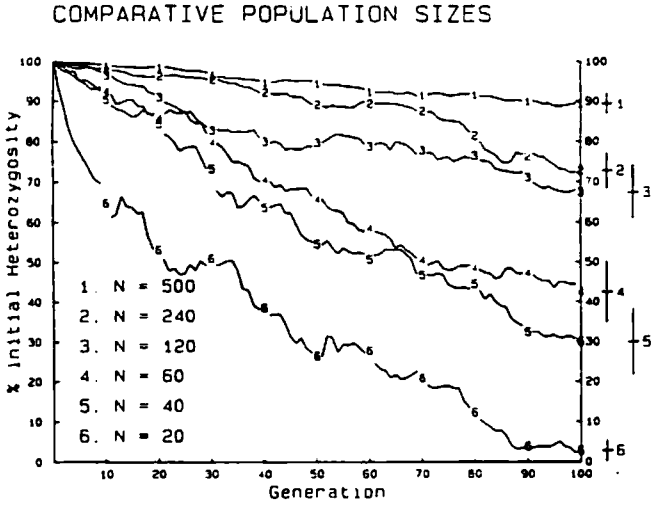

Figure 2. Percent heterozygosity retained in populations of 20, 40, 60, 120, 240, or 500 randomly mating individuals. Each line in this and all subsequent figures represents the average of 25 simulated populations. Means and standard errors of the final heterozygosities are indicated at the right. Except when otherwise specified, all subsequent figures are based on simulated populations of 120 animals.

Putting the loss of genetic variability into a perspective that is meaningful for a species or population of interest can be difficult. The history of inbreeding in a population (Lynch 1977) and the need to adapt to changing environments will affect the loss of heterozygosity that a population can withstand (Selander 1983). To provide some benchmarks, note that inbreeding of 1 percent per generation is considered by animal breeders to have negligible effect (Franklin 1980) and that many human societies prohibit marriages between relatives that would produce offspring with inbreeding coefficients of 6.25 percent or more. (Inbreeding reduces heterozygosity by 1% per 1% increase in the inbreeding coefficient, and losses of heterozygosity due to any kind of population structure are often measured by inbreeding coefficients or F-statistics [Wright 1965, Jacquard 1975]). Experimental populations have responded to artificial selection for more than 75 generations (Falconer 1981), suggesting that sufficient variability exists to allow "adaptation" even after genetic variation has been considerably depleted. Such experimental populations do not cope simultaneously with the diversity of selective constraints that are faced by natural populations, however, and clearly the many species that have gone extinct did not adapt sufficiently and rapidly to changing environments.

Mutation

The ultimate source of new genetic variability is mutation, although recombination, migration, and selection can increase variability within a population by reshuffling existing alleles within and between populations and by changing allele frequencies. Figure 3 shows the effects of mutation on heterozygosity within populations of 120 individuals. Mutation can counter the effects of drift, but not at rates of mutation that are observed in any real population. Mutation rates typically range from 10^{-8} to 10^{-4} per gene per generation in eukaryotes and from 10^{-6} to 10^{-4} in mammals (Hedrick 1983, Strickberger 1985). Only at mutation rates greater than 10^{-3} did new mutation noticeably counter drift in the simulations. (The increased heterozygosity with m = 10^{-4} in Figure 3 was due to chance, not the effects of mutation; note that the higher mutation rate of 10^{-3} had no effect on heterozygosity.)

In part, the minimal effect of mutation in the simulations results from the very high heterozygosity (50%)

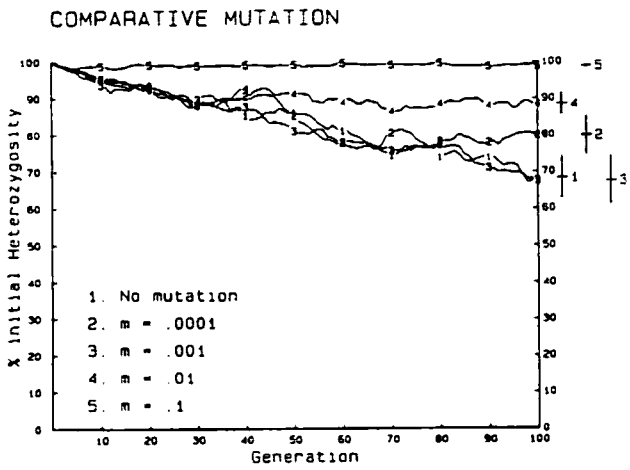

Figure 3. Percent heterozygosity retained in populations with equal forward and backward mutation rates of 0, 10^{-4}, 10^{-3}, 10^{-2}, or 10^{-1} per generation.

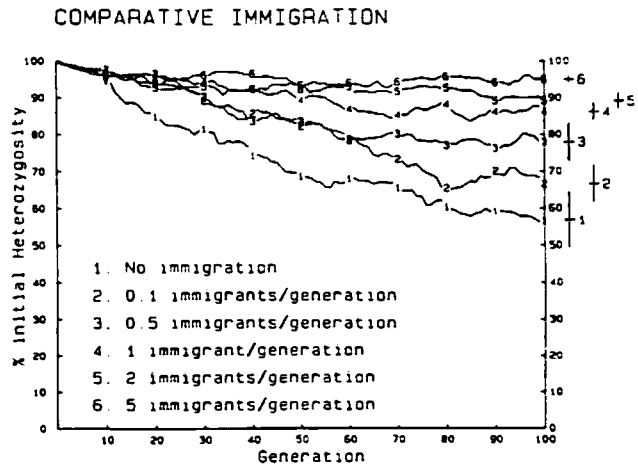

Figure 4. Percent heterozygosity retained in populations receiving an average of 0, 0.1, 0.5, 1, 2, or 5 immigrants per generation from an infinitely large source population with allele frequencies equal to those of the initial populations.

at generation 0. New variation introduced by mutation increases additively, independent of current heterozygosity, while drift leads to a geometric decrease in heterozygosity, the loss being proportional to extant heterozygosity. After heterozygosity reaches a low value, further loss due to drift will have diminished to the rate of gain by mutation: The population will be in mutation-drift equilibrium. For a population of 120 animals with a mutation rate of 10^{-5}, mutation-drift balance is reached when heterozygosity drops to 0.0048, about 1 percent of the initial value in the simulations and about an order of magnitude lower than is commonly observed in natural populations of vertebrates. (In an ideal population such as the one modeled, mutation-drift equilibrium is reached when $H = 4N_em/(1 + 4N_em)$ [Crow & Kimura 1970].)

Immigration

For a captive or otherwise isolated population of a species that retains relatively large populations elsewhere, immigration of individuals from the large source-population constitutes a mechanism, similar to mutation, for reintroduction of genetic variability. Immigration differs in several important respects from mutation, however. Immigration rates can be much greater than are mutation rates. Moreover, immigration is often under control of a population manager. Most importantly, genetic variants introduced into a population by immigration act to restore alleles that formerly existed in the captive population or the ancestral stock from which it was derived.

Effects on heterozygosity of immigration from a hypothetical, genetically unchanging, source-population into a population of 120 individuals are shown in Figure 4. Given the standard errors observed around final heterozygosities, there is no evidence that an immigration rate of 0.1 immigrants or less per generation causes a biologically significant effect.

Immigration rates as low as 0.5 immigrants per generation, obtainable for many captive propagation efforts, strikingly reduce the loss of variability from small populations. Although it is not obvious in Figure 4, the immigration causes genetic variation to approach an asymptote: The farther from the initial state a population becomes, the greater the restorative effect of immigration. Therefore, immigration can bring a formerly isolated and considerably divergent population back toward the genetic condition of the source population.

Because the degree to which immigration restores heterozygosity is dependent upon the extent to which the population has diverged from the source population, the effect of immigration is much greater on smaller populations than on larger populations. With moderate rates of immigration, the long-term (asymptotic) genetic fate of a population is almost independent of population size (Fig. 5).

Selection

Three types of selection were modeled: directional selection in which one homozygote has superior fitness to the other and the heterozygote has intermediate fitness, balancing selection in which the heterozygote has superior fitness and the two homozygotes have equal fitness, and disruptive selection in which the heterozygote has inferior fitness and the two homozygotes have equal fitness. As expected, under strong selection (Fig. 6A: relative fitnesses of 1.0 : 0.8 : 0.6 for directional selection; 0.8 : 1.0 : 0.8 for balancing selection; and 1.0 : 0.8 : 1.0 for disruptive selection), balancing selection maintains allele frequencies and heterozygosity,

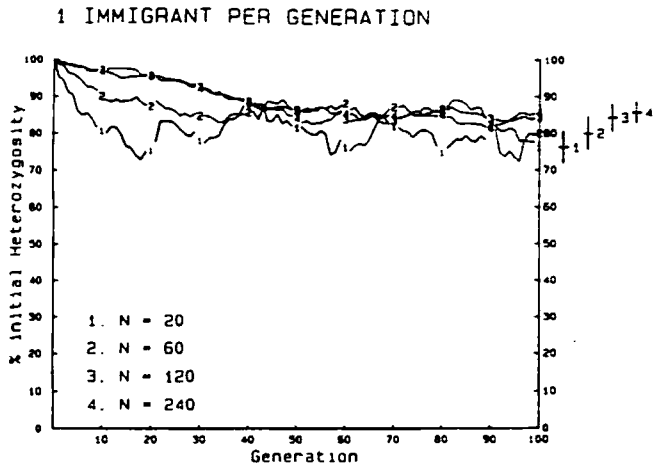

Figure 5. Percent heterozygosity retained in populations of size 20, 60, 120, or 240 receiving 1 immigrant per generation from a source population.

while directional and disruptive selection rapidly fix one allele in each population and thereby deplete genetic variation. Under symmetrical disruptive selection, about half the populations are fixed for one allele and half are fixed for the other. All populations were fixed for the selectively favored allele under directional selection.

Fitness differentials of 20 percent are probably rare, although such strong natural selection has been reported for some polymorphic traits (Endler 1986). Under more moderate selection (relative fitness of 1.0 : 0.95 : 0.90 for directional selection; 0.95 : 1.0 : 0.95 for balancing selection; and 1.0 : 0.95 : 1.0 for disruptive selection), the trends in heterozygosity are the same, but diminished (Fig. 6*B*). Over five to 10 generations, a 5 percent fitness differential has little effect on levels of genetic variation. Weak selection pressures (Fig. 6*C*, relative fitnesses of 1.0 : 0.99 : 0.98 for directional selection; 0.99 : 1.0 : 0.99 for balancing selection; and 1.0 : 0.99 : 1.0 for disruptive selection) affect heterozygosities, but the effects are hardly discernible over the background noise of random drift. This is in accord with analytical results of Kimura (1955), Robertson (1962), and others (Crow & Kimura 1970, Wright 1969) that show that selection is effective over random genetic drift when the product of the effective population size and the selection coefficient is much greater than one.

Population Subdivision

Captive populations are often fragmented into partially or wholly isolated subpopulations, each consisting of a breeding population held by a zoo or a group of zoos in close geographical proximity or in close cooperation. One effect of this subdivision is to allow genetic differentiation to develop between subpopulations, as a result of genetic drift or differential selection on the subpopulations inhabiting different environments (Chesser et

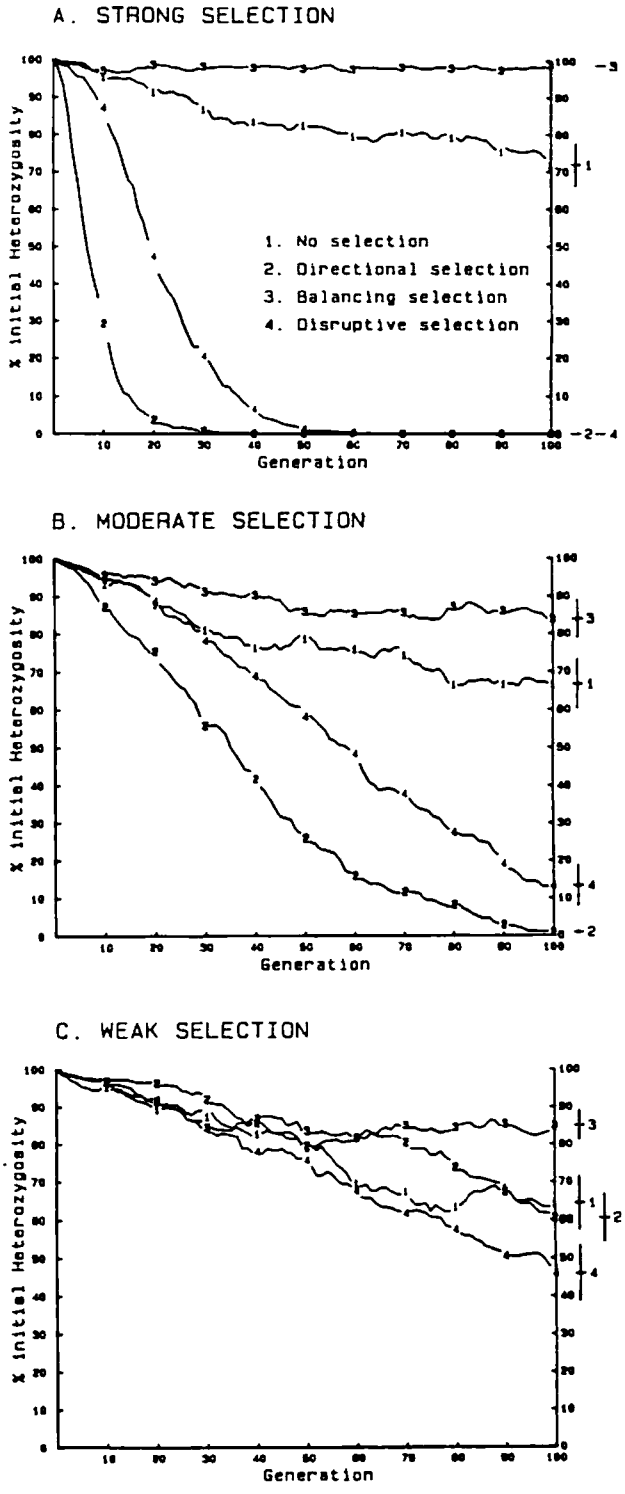

Figure 6. Percent heterozygosity retained in populations subjected to no selection, balancing selection, disruptive selection, or directional selection. (A) *strong selection (relative fitnesses of 0.8 : 1.0 : 0.8, 1.0 : 0.8 : 1.0, and 1.0 : 0.8 : 0.6);* (B) *moderate selection (relative fitnesses of 0.95 : 1.0 : 0.95, 1.0 : 0.95 : 1.0, and 1.0 : 0.95 : 0.90);* (C) *weak selection (relative fitnesses of 0.99 : 1.0 : 0.99, 1.0 : 0.99 : 1.0, and 1.0 : 0.99 : 0.98).*

al. 1980). Furthermore, because the subpopulations are necessarily smaller than is the total population and because each subpopulation would occupy a narrower range of habitats than does the total population, two processes that deplete genetic variation will be enhanced in isolated subpopulations relative to a panmictic population. Genetic drift will inevitably be greater in fragmented subpopulations; and while heterogeneous selection on large populations utilizing diverse habitats can maintain genetic variation (Levene 1953, Levins 1968, Hedrick et al. 1976, Taylor 1976, Lacy 1982), directional selection on isolated subpopulations for traits advantageous in narrow habitats would deplete variation (Karlin 1982).

Figure 7 illustrates the effect of dividing a population of 120 individuals into one, three, five, or 10 fully isolated breeding units. Average within-subpopulation heterozygosities (shown by points unconnected by lines) are strikingly diminished when the population is fragmented, while total gene diversity within and between subpopulations (points connected by lines) is better maintained by population subdivision.

Total gene diversity in a highly fragmented population asymptotes at a high level. In each generation some of the variation formerly present within each subpopulation is converted to variance between populations as the subpopulations randomly diverge. This between-subpopulation variation is then protected from further decay due to genetic drift. When subpopulations become totally inbred (no heterozygosity within subpopulations), total variation is fixed at a level equal to the between-subpopulation genetic variation. Maintenance of total variation in simulated populations depends on the persistence of each subpopulation at a constant size,

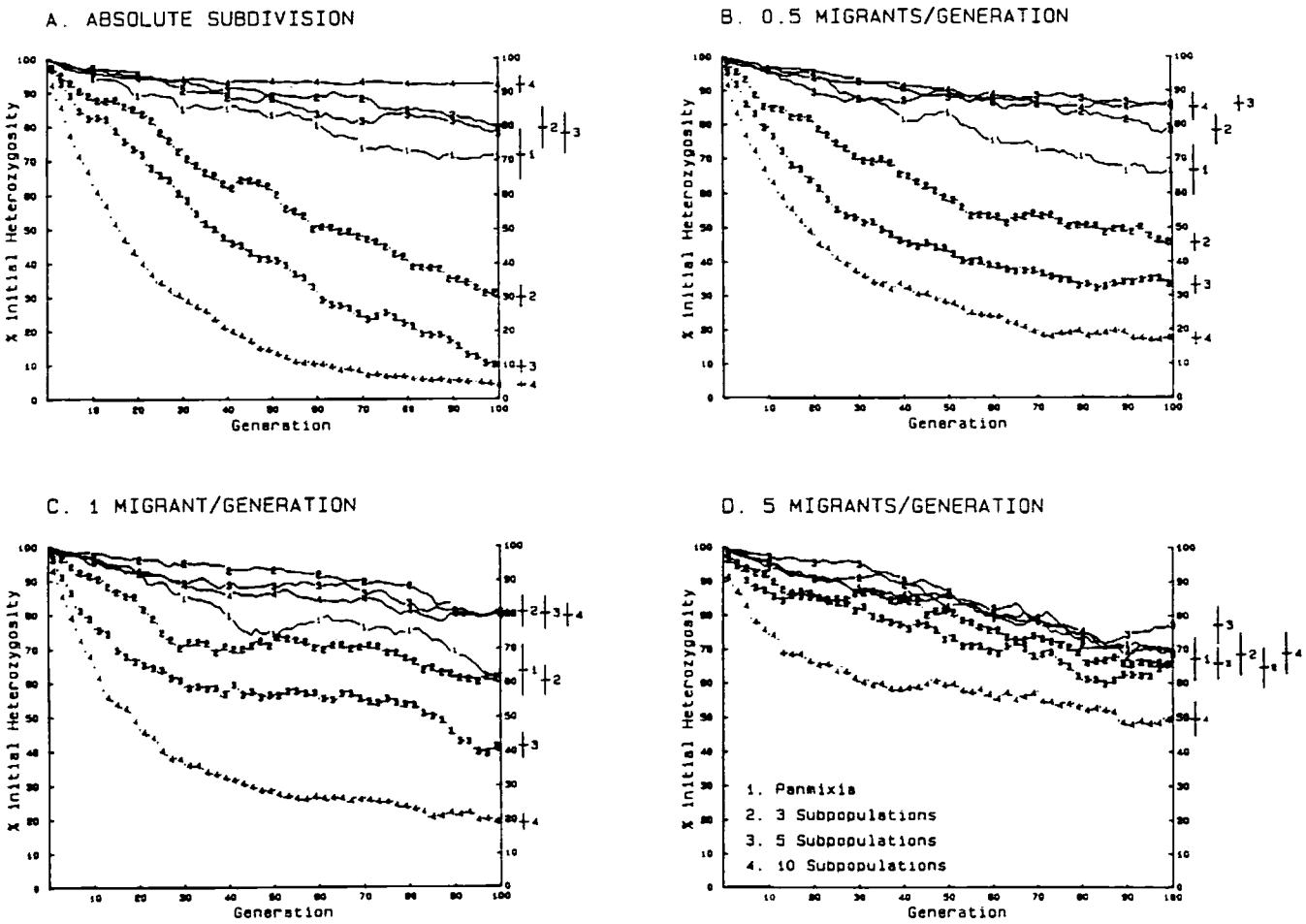

Figure 7. Percent heterozygosity retained within subpopulations (points and numbers not connected by lines) and total heterozygosity retained within and between subpopulations (points connected by lines) in populations of total size 120 divided into 1, 3, 5, or 10 subpopulations. (A) *no migration between subpopulations;* (B) *0.5 inter-subpopulation migrants per generation;* (C) *1 migrant per generation;* (D) *5 migrants per generation.*

however. If some subpopulations were to go extinct, some between-population diversity would be lost with them.

Subpopulations need not be totally isolated. As few as 0.5 inter-subpopulation migrants per generation (over all subpopulations, not per subpopulation) will reduce inbreeding within subpopulations (compare within-subpopulation heterozygosities in Fig. 7*B* to those in 7*A*). Higher rates of migration between subpopulations (Fig. 7*C* and 7*D*) bring both the within-subpopulation heterozygosities and the total gene diversities closer to the heterozygosity expected under panmixia. Theoretical analyses (Wright 1969) and simulations (not shown) demonstrate that the effect of migration between populations on preventing divergence among subpopulations is dependent upon the number of migrants per generation, and independent of total population size.

Migration reintroduces genetic variation to subpopulations, causing within-subpopulation heterozygosities to level out after an initial rapid decline. (As was the case for immigration from an external population, migration between subpopulations only becomes effective after populations have diverged and lost variability.) By preventing subpopulations from becoming fixed with different genetic compositions, migration also prevents the subdivided population structure from retaining large total gene diversity. Under high rates of migration (Fig. 7*D*) subdivided populations do not retain within-subpopulation variation as well as do panmictic populations, nor do they retain measurably more total variation.

Figure 8 compares the effects of different rates of migration between subpopulations of a population divided into five breeding units of 24 individuals. Increasing migration lessens inbreeding within subpopulations, though not until generation 10 or beyond. Very low levels of migration perhaps actually increase total genetic variation maintained relative to the no migration case, while higher rates of migration bring total heterozygosity down.

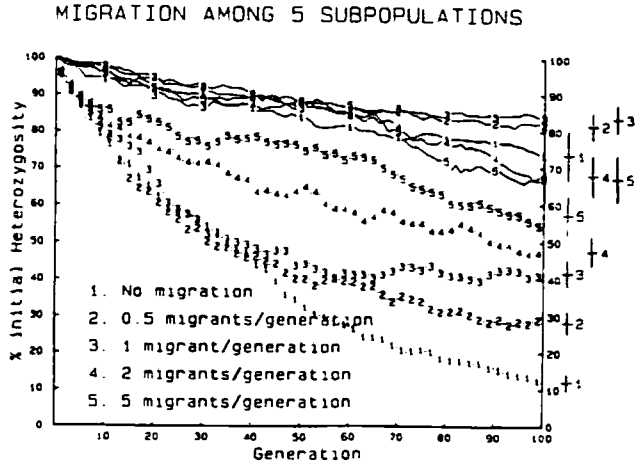

Figure 8. Percent heterozygosity retained within subpopulations (points not connected by lines) and total heterozygosity retained within and between subpopulations (points connected by lines) in populations divided into 5 subpopulations with an average of 0, 0.5, 1, 2, or 5 inter-subpopulation migrants per generation.

Interaction Between Selection and Population Subdivision

By augmenting genetic drift within subpopulations, subdivision alters the effectiveness of selection on small populations. Strong directional selection usually overwhelms genetic drift (Fig. 9*A*), even in highly subdivided populations. (About 1 percent of subpopulations of 12 individuals will be fixed for an allele strongly opposed by selection.) With more moderate selection, genetic drift within subpopulations prevents selection from being wholly effective (Fig. 9*B*). Among subpopulations of 12 individuals each, an average of 22 percent became fixed for the allele whose homozygote had 10 percent lower fitness than did the other homozygote. The selectively disadvantageous allele also remained longer within subpopulations of 24 and 40 individuals (five and three subpopulations, respectively) than it did within a panmictic population of 120. Weak directional selection (not shown), with only minor effects on a panmictic population, had no effect on the fate of alleles in subdivided populations.

The heterozygosity-preserving effects of balancing selection are also diminished by drift within small subpopulations (Figs. 9*C* and 9*D*). Balancing selection slows, but does not stop, fixation of alleles in small subpopulations, therefore also countering potential advantages of population subdivision. Rather than maintaining total heterogeneity by furthering between-subpopulation genetic differentiation, subdivision of a population under balancing selection causes a greater loss of total heterozygosity than would occur if the population were panmictic.

Discussion

Flesness (1977), Denniston (1978), Chesser et al. (1980), Allendorf (1983), Chesser (1983), Fuerst and Maruyama (1986), and Foose et al. (1986) have made recommendations about the optimal genetic management of captive populations. The simulations presented here provide further basis for making decisions about the genetic management of small populations. The goal of presenting simulations is not to prescribe a population size and structure to be used in the management of all populations: The opportunities, constraints, and goals of captive propagation programs are too diverse to permit such broad recommendations. Simulations, however, can help

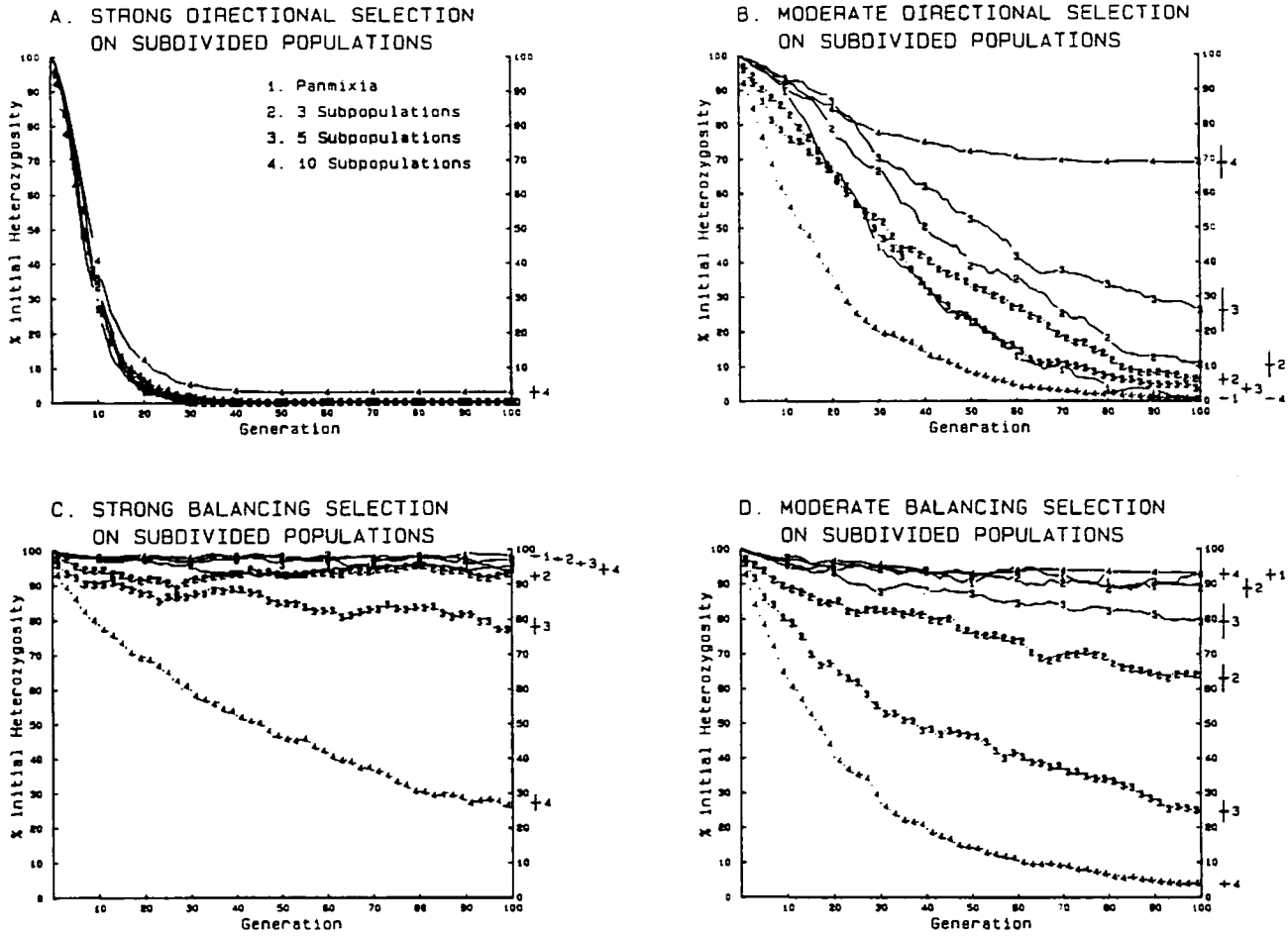

Figure 9. Percent heterozygosity retained within fully isolated subpopulations (points not connected by lines) and total heterozygosity retained within and between subpopulations (points connected by lines) in populations divided into 1, 3, 5, or 10 subpopulations subjected to selection. (A) *strong directional selection (relative fitnesses of 1.0 : 0.8 : 0.6, except for total heterozygosity in 10 subpopulations, all heterozygosities have mean and standard error zero by generation 50);* (B) *moderate directional selection (relative fitnesses of 1.0 : 0.95 : 0.90);* (C) *strong balancing selection (relative fitnesses of 0.8 : 1.0 : 0.8);* (D) *moderate balancing selection (relative fitnesses of 0.95 : 1.0 : 0.95).*

to define the effects that different management strategies will have on the genetic constitution of a population. With such knowledge, management plans can become tailored, informed attempts to achieve the long-term genetic goals of captive propagation.

Genetic drift is commonly the most powerful evolutionary force acting on small populations, so, to a first approximation, management concerns can be focused solely on effects of drift. Under stringent conditions of selection and/or population structure, imposed artificially or naturally, other evolutionary forces can overcome the stochastic effects of drift. Genetic drift is a sampling phenomenon, and thus can be most effectively contolled by keeping large (effective) breeding populations. In unmanaged populations, many individuals contribute little or nothing to future generations, and careful management of a population is usually necessary to assure that the genetically effective population size is not greatly smaller than the censused population (Foose 1977, Flesness 1977, Foose et al. 1986). Chesser (1983) points out that increases in the effective population size by demographic management may not be sufficient to slow drift adequately, and even suggests that "exclusive focus on population size can have disastrous results for the management of genetic resources." He then paradoxically discusses various means of managing the demography of a population to increase the effective population size (by managing migration between subpopulations) and thereby decrease inbreeding.

Mutation can reasonably be ignored as an evolutionary force in small captive populations. For example, a captive population of 100 individuals is unlikely to experience a mutation in any individual at more than 10 percent of its genetic loci over 100 generations. More-

over, the minor additional variation inserted into a captive population by mutation over any timespan of human interest is likely to be counterproductive for the goal of preserving the genetic uniqueness of a population.

One approach to the question of what size captive population is needed to preserve sufficient variability for long-term viability is to determine the number that would maintain adequate heterozygosity when at mutation-drift equilibrium. For example, Franklin (1980) suggested that a population of 500 would be sufficiently large to be in mutation-drift balance for adequate variability of quantitative (polygenic) traits. (Franklin's estimate was based on papers by Lande [1976] and others that suggested mutation could maintain considerable variation for quantitative traits under moderate stabilizing selection. Turelli [1984] questioned Lande's conclusions, showing that with somewhat different [and perhaps more realistic] assumptions about mutation rates, phenotypic effects of mutation, and the intensity of selection, mutation is much less capable of maintaining variation in a selected trait.) Franklin's estimate has often been proposed as a guideline for management of endangered species (e.g., Soulé & Wilcox 1980, Frankel & Soulé 1981, Schonewald-Cox et al. 1983) and has been applied to management plans for the Siberian tiger (Foose & Seal 1981, Foose 1983).

The use of a mutation-drift equilibrium model, or perhaps any equilibrium model, for the management of small captive populations may be misguided, however. At equilibrium, heterozygosity remains constant, but the genome does not. Allelic losses still occur due to drift, but those alleles are replaced by new, generally different mutations. In a natural population, most new mutations are lost by drift, a few increase to sufficient frequencies to be subject to the positive or negative force of selection, and the population slowly evolves. In a captive environment, such changes also occur, but selection is likely to be very different from that experienced by a population living in a more natural habitat. While in mutation-drift equilibrium, a captive population may be rapidly evolving into something quite different genetically from what it was initially. Unless captive propagation seeks to create domesticated stocks or to make specific changes in the genetic make-up of a population, genetic captive-management plans should aim for a cessation of evolutionary processes to the extent possible. (Planned genetic alteration of a population might occasionally be necessary to assure survival in captivity or other highly modified environments, and this consideration may override concerns about preservation of an unaltered population [Templeton & Read 1983, Foose et al. 1986].)

For assessing success in preserving the genetic characteristics of a population, captive management plans should be concerned with the loss of the variation present in the founding population. The consensus that arose from the 1984 Front Royal conference to strive for a retention of 90 percent of heterozygosity for 200 years (Soulé et al. 1986) reflects a recognition of the non-equilibrium nature of genetic management of captive populations.

Fuerst and Maruyama (1986) also stressed the lack of equilibria in early generations of captive breeding, pointing out that most rare alleles present in natural populations would not be sampled when a small number of founders is obtained to begin captive breeding, or would be lost within the first few generations of captivity. Because rare alleles are lost during bottlenecks much more rapidly than is heterozygosity, Fuerst and Maruyama (1986) recommend that emphasis be placed on the preservation of allelic diversity and, therefore, that larger founding populations than those suggested by studies of heterozygosity will be needed. Unfortunately, except for short-term captive propagation plans, it is unlikely that sufficient wild stock can be obtained and sufficient captive stock maintained to give much hope for the preservation of rare alleles. Managers of very small populations may be forced to focus efforts on minimizing the deleterious consequences of severe loss of heterozygosity.

If a large wild population exists and can be used to supplement the captive population, periodic immigration (capture of new founder stock) can drastically reduce drift of the captive population away from the genetic characteristics of the wild population. As few as one immigrant per two generations would be beneficial, and five or more immigrants per generation would virtually halt genetic drift within the captive population. Immigration into very small populations is especially effective (and important), as loss of genetic variability is almost independent of population size when immigrants are introduced at a rate of one or more per generation. A population of only 20 individuals that receives an immigrant per generation retains almost as much genetic variability as does a population an order of magnitude larger. Because immigration reverses extant genetic differentiation between captive and source populations, sporadic immigration at the same long-term average rate can be just as effective as is a regular schedule of immigration in maintaining a population close to its initial state.

For an endangered species, there may be no large source-population available. If the captive population is much larger than is the wild population (as with Siberian tigers), migration into the wild population from the captive population can help to maintain genetic variability in an endangered wild population that otherwise might experience excessive inbreeding. If both the wild and captive populations are small, migration between them could give to both some of the advantages of a population size equal to their combined numbers *(see results and discussion concerning population subdivision)*.

Selection can deplete, maintain, or even augment genetic variation, yet magnitudes of selection likely to act on populations not under artificial selection are not ef-

fective when populations are of a size typical of captive populations. The inefficiency of selection in the face of rapid genetic drift suggests that some concerns and some hopes of captive propagation are unlikely to be realized. The altered environment of captivity creates new selective pressures not experienced by a natural population, and releases the captive population from selective constraints experienced by the wild counterpart. Unless some traits are strongly deleterious or advantageous in a captive environment (causing perhaps a 10% differential in mortality between those individuals with the traits and those without), response to selection for "captive" traits is unlikely to be apparent amid random fluctuations in allele frequencies. Inadvertent and unavoidable selection for domestication has probably not produced "zoo species" in which genetic characteristics important to survival in the wild have been selected away. (Behavioral changes in captive populations are much more likely to cause problems for reintroduction programs.)

Unfortunately, the inefficiency of selection also means that drift will often fix deleterious alleles by chance in small captive populations. Genetic variants poorly adapted to either a captive or wild habitat may become prevalent in long-term captive populations. If continued survival and propagation of a species seems threatened by genetic changes occurring in the captive population, it may be necessary to impose strong artificial selection for a zoo-adapted, domesticated animal.

By dividing a captive population into several subpopulations (management units for breeding loans, trades, and sales), more of the genetic variability originally present in the founding stock can be maintained overall. The genetic cost of population subdivision is increased inbreeding within each subpopulation, and greater divergence of individual subpopulations from the genetic characteristics of the founders (Chesser et al. 1980, Chesser 1983).

The frequency of movement of animals between captive populations determines whether a species is managed as one interbreeding population or a number of more or less isolated subpopulations. An often-cited (e.g., Spieth 1974, Frankel & Soulé 1981, Hedrick 1983, Foose et al. 1986) theoretical result is that when the number of migrants per generation much exceeds one, the subdivided population behaves as though it were panmictic (Moran 1962). As shown in Figure 7*D* and Figure 8, however, five migrants per generation are not sufficient to bring the population to effective panmixia. Even 20 migrants per generation were not sufficient to prevent fully loss of genetic diversity within, and divergence among, subpopulations (simulations not shown). Allendorf and Phelps (1981) found that 10 migrants per generation were insufficient to prevent significant divergence among subpopulations in their very similar computer model of genetic drift in subdivided populations. The difference between 20 and "greater than one" may not be important to the theoretical results, but it certainly has meaning to the population manager.

Fuerst and Maruyama (1986) considered the fate of allelic diversity in subdivided populations. Pointing out that rare alleles are likely to be lost in small populations (even if substantial heterozygosity remains), and that most subpopulations would retain only the common alleles of the source population, they suggested that population subdivision is not beneficial to the preservation of allelic diversity. To the contrary, a subdivided population structure may be the only way to preserve allelic diversity in small populations. In the absence of balancing selection, eventually all alleles but one would be lost at each genetic locus of an isolated population. The probability that a neutral allele will be retained is equal to its initial frequency. Thus, a neutral allele with initial frequency in the source population of 0.01 has a 1 percent chance of being sampled and retained in any population. If 10 subpopulations are maintained, the probability that at least one will retain a rare allele is about 10 times the probability that a single panmictic population would retain the allele. (In the extreme, a clonally reproducing organism, with as many subpopulations as individuals, would never lose allelic diversity so long as all lines were maintained.)

Even in the first few, nonequilibrial, generations, a subdivided population will retain allelic diversity better than would a panmictic population. The probability that a rare allele is initially sampled from the wild population is not dependent upon how founders are partitioned into breeding groups for production of future generations. After the initial sampling, rare alleles will be present at much higher frequencies in those subpopulations where they exist than they would have been in a panmictic population, and this helps protect them from random loss. Mathematically, the probability of loss from a randomly mating population in any one generation is $(1 - p)^{2N}$, in which p is the allele frequency and 2N is the number of alleles in the population. The probability of loss in any one generation from all k equal-size subpopulation is

$$(1 - p_1)^{2N/k} \cdot (1 - p_2)^{2N/k} \cdot \ldots \cdot (1 - p_k)^{2N/k}$$
$$= [(1 - p_1) \cdot (1 - p_2) \cdot \ldots \cdot (1 - p_k)]^{2N/k}$$
$$= [\text{geometrical mean of } (1 - p_i)]^{2N},$$

in which p_i is the frequency of the allele in subpopulation i. The frequency of any allele in the panmictic population will be equal to the arithmetic mean frequency across the subpopulations, $([1 - p_1) + (1 - p_2) + \ldots + (1 - p_k)]/k = (1 - p))$, and thus the probability of loss from the panmictic population is [arithmetic mean of $(1 - p_i)]^{2N}$. The goemetric mean of a series of numbers is smaller than or equal to the arithmetic mean. Thus the probability of loss from all subpopulations is always less than the probability of loss from the one panmictic

population. Contrary to Fuerst and Maruyama (1986), perhaps the most beneficial result of population subdivision is the greater conservation of allelic diversity.

Population subdivision also slows the genetic response of a population to selection because it increases genetic drift within subpopulations where selection would act. By inhibiting directional selection, subdivision will help maintain variability and will slow inadvertent domestication of captive stocks. (If whole subpopulations were selectively eliminated after subpopulations have diverged [between-population selection], perhaps with the intent of eliminating less successful stocks, there would be considerable loss of genetic diversity.) Although not modeled here, different selection pressures among subpopulations can also maintain genetic variability (reviewed by Hedrick et al. 1976, Karlin 1982).

To the extent that balancing selection (favoring heterozygotes within each population) maintains genetic variability (an issue under much debate among evolutionary biologists), the increased drift that occurs with subdivision will push populations away from equilibria maintained by balancing selection and thereby cause loss of adaptive genetic variability. The disruption of balanced equilibria by drift is simply a restatement, in causal terms, of the deleterious effects of inbreeding ("inbreeding depression") in subdivided populations. Concern about the reduced efficacy of balancing selection should be tempered, however, by the realization that natural selection on captive populations is probably quite different from natural selection on wild populations. Polymorphisms maintained by balancing selection in the wild may not be protected by balancing selection in captive populations.

Chesser et al. (1980) suggested a management scheme for using subdivision to maximize balancing selection in order to preserve polymorphism in small populations. In examining equilibrium models of polymorphism, they point out that polymorphism can be maintained indefinitely in a small population only if there is strong balancing selection. They proposed to let subpopulations become partially inbred, so that the general heterosis (hybrid vigor) produced with subsequent migration would result in temporary strong balancing selection on the genome. If there is much variation that is not strongly adaptive in a captive environment, however, or if the time scales of conservation goals are finite (on the order of tens to perhaps hundreds of generations), then practices aimed at slowing evolutionary processes are probably more desirable.

Slatkin (1981) presented both analytical and simulation analyses of the efficacy of selection in a subdivided population with migration between subpopulations. He found that when migration is low (less than about 0.5 per generation), the ultimate result of selection (probability of fixation of a favored allele) is quite similar to the case of minimal migration; when migration is much above one per generation, the ultimate response was usually similar to the case of a panmictic population. The times to fixation (i.e., the rate of response rather than the ultimate result of selection) always increased with decreasing migration between subpopulations. Thus, as would be expected from the simulation results presented here, increasing isolation of the subpopulations slowed the rate of evolutionary change.

Allendorf (1983) recommended a management strategy of 1 migrant per generation among isolated nature reserves, pointing out that low levels of migration prevent the total loss of alleles from local populations, while not preventing adaptive genetic divergence. My simulations suggest that that level of migration might be advantageous among small captive populations also, although the costs and benefits of subdivision of captive populations are perhaps somewhat different from those for populations managed in nature reserves. Random genetic divergence between subpopulations allows for better maintenance of alleles and total gene diversity, but local adaptation of subpopulations resulting from differential selection might be an unfortunate consequence of captive propagation programs aimed at eventual restoration of diverse gene pools in more natural habitats. (As pointed out above, however, I see selection as relatively inefficient in small subdivided populations.) Also, while Allendorf emphasizes preventing the total loss of allelic variants from populations, I worry more about potentially severe losses of heterozygosity and any consequent loss of fitness. Reintroduced populations and augmented remnant wild populations will need both allelic diversity and moderate levels of heterozygosity to become securely reestablished.

The value of population subdivision to captive propagation depends considerably on the time scale for which captive management goals are set. The genetic cost of subdivision occurs primarily in early generations, as inbreeding is especially rapid over the first 10 to 20 generations. The benefit of improved maintenance of total variability and the ability of between-subpopulation migration to reduce inbreeding both become apparent only after 10 to 20 generations, because both are dependent upon genetic divergence of subpopulations. For short-term management plans, there would be no genetic advantage to subdivision of the population, although isolation of smaller breeding groups may be important in the prevention of catastrophic disease outbreaks. For very long-term management (30 or more generations), the optimal management plan might be to subdivide the captive population into units of perhaps 20 breeding individuals each and then carefully to regulate inter-unit migration at the lowest level that does not lead to unacceptably deleterious effects of inbreeding. Apparently

more concerned about the effects of inbreeding, Foose et al. (1986) recommended keeping subpopulations sizes greater than 25, and preferably between 50 and 100. Unfortunately, the maximum acceptable level of inbreeding almost certainly differs among species. Currently, information does not exist for any species that would allow accurate determination of the degree of inbreeding that would jeopardize long-term survival.

Population subdivision is reversible, however, up to the point that one or more subpopulations go extinct. If a preliminary plan for subdivision seemed not to be producing desired results, subpopulations could be merged to produce a panmictic population that almost always would be more diverse genetically than it would have been had it never been subdivided. Unfortunately, such a reconstituted panmictic population, while high in genetic diversity and with allele frequencies approximating those in the founders, may be rather different from the ancestral stock with respect to genetic linkage relationships. On the other hand, if a captive population is kept panmictic there is no way to recover genetic variants that are lost by drift without introducing new founder stock from the wild.

Perhaps the biggest difficulty in a management plan centered around a divided breeding population lies in administration. Moderate levels of migration cancel the genetic benefits of subdivision, and more quickly so than the genetic costs of inbreeding are removed. For population subdivision to be a useful management tool, movement of animals between breeding units must be strictly controlled. Two or three unplanned movements per generation could turn genetic benefits into costs. For example, a highly subdivided population (10 subpopulations of 12 individuals each) with high migration rates (5 to 10 migrants per generation over the total population) will suffer effects of moderate inbreeding within subpopulations and yet likely retain no more total gene diversity than would a panmictic population. Unfortunately, many captive breeding programs currently result in just such a population structure. Given the primitive state of knowledge about the effects of population subdivision, management plans need to be carefully monitored and revised when necessary.

A preliminary attempt has been made to use computer simulations to explore some genetic consequences of evolutionary forces acting on managed populations. Much more detailed examination of the genetics of small populations is possible by computer simulation. There is perhaps a greater need at this point, however, to obtain empirical data on genetic responses by particular species of interest. If possible, work should focus on developing generalizations that allow prediction of the genetic behavior of a population based on knowledge of its biology and the biology of taxonomically and ecologically similar organisms. As empirical data on the effects of inbreeding, the importance of genetic variation to captive and wild populations, and the factors maintaining or depleting variation are gathered, computer modeling can focus on factors of most importance, using appropriate parameters. Computer models such as the one presented here can be useful almost immediately in the comparison of possible alternative management plans being considered for species propagated in captivity.

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EVOLUTIONARY BIOLOGY

Douglas J. Futuyma

B The Wahlund Effect: Genotype Frequencies in a Subdivided Population

Suppose a "population" consists of k subpopulations, each with a different gene frequency p_i. Among the subpopulations the mean gene frequency is $\bar{p} = \Sigma_i p_i/k$, and the variance in gene frequency is $V_p = \Sigma_i (p_i - \bar{p})^2/k$. Now note that V_p is

$$\frac{\Sigma_i(p_i^2 - 2p_i\bar{p} + \bar{p}^2)}{k} \text{ or } \frac{\Sigma_i p_i^2 - 2\bar{p}\Sigma_i p_i + \bar{p}^2}{k}$$

But $\Sigma p_i = k\bar{p}$, so $V_p = \Sigma_i p_i^2/k - \bar{p}^2$. Thus $\Sigma_i p_i^2/k = \bar{p}^2 + V_p$. But $\Sigma_i p_i^2/k$ is the average proportion of AA homozygotes among the subpopulations, the proportion of AA in the population as a whole. Thus the frequency of this homozygous class exceeds the Hardy-Weinberg frequency ($\bar{p}^2$) by an amount V_p. Similarly the frequency of $A'A'$ in the entire population is $\bar{q}^2 + V_p$, and the frequency of heterozygotes is, by subtraction, $2\bar{p}\bar{q} - 2V_p$. This disparity between observed frequencies and Hardy-Weinberg frequencies is termed the Wahlund effect.

This result implies that an investigator who samples from what appears to be a single panmictic population, but is actually an aggregate of subpopulations that vary in gene frequency, will find an unexpected deficiency of heterozygotes. The magnitude of this deficiency is indeed a measure of the degree to which the "population" is actually structured into subpopulations (or, a measure of the variance in gene frequency among the subpopulations). Another such measure, of course, is F; the frequency of heterozygotes may be written either $2\bar{p}\bar{q} - 2V_p$ or $2\bar{p}\bar{q}(1 - F)$. Equating these, we find that $2(\bar{p}\bar{q} - V_p) = 2(\bar{p}\bar{q} - \bar{p}\bar{q}F)$, or $F = V_p/\bar{p}\bar{q}$.

This F, denoted F_{ST}, is different from the F that represents the average inbreeding coefficient of individuals derived from consanguineous matings within a subpopulation. It is useful to recognize, as Wright (1965) does, several levels of F:

- F_{IS} the probability that two gametes taken at random within an average subpopulation yield an autozygous individual
- F_{ST} the probability that two gametes taken at random from two different subpopulations yield an autozygote
- F_{IT} the probability that two gametes taken at random from the entire "population" yield an autozygote

Wright shows that the relationship among these can be written $F_{ST} = (F_{IT} - F_{IS})/(1 - F_{IS})$.

THE EFFECT OF GENE FLOW

Probably few populations are completely isolated. The greater the amount of gene exchange among populations, the more similar their genetic composition will be, unless other factors counteract migration's homogenizing influence.

One such factor is natural selection, which maintains a permanent disparity in the gene frequencies of different populations if different alleles are favored in the various populations (*Box C*). This is reflected in many patterns of adaptive geographic variation. But if migration is strong enough, it can counteract selection to at least some extent, preventing a population from becoming fully adapted to its environment. For example, adult water snakes (*Natrix sipedon*) on the Lake Erie Islands are uniformly grayish in color, whereas mainland adults are strongly banded (*Figure 12*). Among young island snakes, however,

Breeding Plans for Small Populations, Based on the Dynamics of Quantitative Genetic Variance

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Habitat destruction and fragmentation will often make it necessary to protect small populations in nature preserves or to establish captive breeding programs to prevent their extinction. In most wild populations, ecological factors are likely to be more important than genetic factors in determining the probability of persistence into the forseeable future. This is because a wild population that can avoid extinction from Allee effects, edge effects, demographic and environmental stochasticity, and local extinction and colonization is also likely to be large enough to prevent appreciable inbreeding depression or loss of genetic variability from random genetic drift (Lande 1988). However, in wild populations artificially reduced to a small size, genetic factors, and their interactions with ecological factors, become increasingly important.

In the captive environment, demographic fluctuations caused by predation, diseases, weather and food supply can be at least partially controlled. If the goal of the captive breeding program is captive release into the wild at a later date, the breeding structure and size of the population can be managed to maintain a high proportion of the original genetic variability present in the wild population from which it was established. This is likely to increase its chance of survival upon reintroduction to the wild, since additive genetic variance is necessary for adaptation to a changing environment. Genetic considerations should therefore play a dominant role in breeding plans for captive populations with this goal. However, even in a carefully controlled environment, demographic factors such as population growth rate, age distribution and sex ratio should not be ignored (Foose 1980).

Soulé et al. (1986) proposed for captive populations the management goal of maintaining 90% of the genetic variability present in the original (base) population for a period of 200 years. Using a model of an ideal population with discrete, nonoverlapping generations and a Poisson distribution of progeny numbers, they computed by numerical methods the final or equilibrium population size that would be necessary to achieve the goal with a certain initial number of founders for a species with a given population growth rate

and generation time, assuming geometric growth of the population up to the final size. Their model accounted for the loss of genetic variability (i.e., heterozygosity or purely additive genetic variance in quantitative traits) caused by random genetic drift in a finite population. Already this or similar goals, and the breeding plans recommended by Soulé et al. (1986) to meet them, have been adopted in management plans for captive populations of several endangered species (e.g., for the gorilla, cheetah, addax, Asian wild horse, scimitar-horned oryx, greater one-horned Asian rhinoceros, and Florida panther [plans available from AAZPA Conservation Director]).

Most morphological, behavioral and physiological measurements are genetically complex (polygenic) quantitative traits, which are generally thought to be of critical importance in adaptation to natural environments (Franklin 1980; Lande and Barrowclough 1987). Here we investigate the influence of additional factors affecting the maintenance of additive genetic variance in quantitative characters, i.e. mutation, immigration from the wild, selection in the captive environment, and population subdivision. It is shown that these factors permit smaller final population sizes and founder numbers necessary to achieve the goal of preserving a certain fraction of the original genetic variability for a particular period of time. By using a continuous time model, which is probably more accurate than the discrete generation model for most real populations with overlapping generations, it is possible to derive general analytical solutions that allow breeding plans to be specified for management goals involving the maintainance of any fraction of the original genetic variability for any time period. The text develops the general models and provides explicit evaluations in graphical form for the particular management goal suggested by Soulé et al. (1986). Analytical formulas are presented in the Appendix.

Dynamics of additive genetic variance in quantitative traits

In the captive environment natural selection on most traits is likely to be greatly reduced or absent, so that random genetic drift and mutation are the most important factors affecting

genetic variation in a population closed to immigration. Nevertheless, there may be substantial selection on some characters for adaptation to captivity, and evolutionary changes resembling domestication are likely to occur in captive populations, e.g. selection for docility and high reproduction (Arnold, this vol.). We first analyze random genetic drift and mutation in a population founded from a given initial number of individuals which grows to a constant final number. Immigration, selection, and subdivision in a population of constant size are then analyzed.

Random genetic drift and mutation

Let V_g be the (purely) additive genetic variance in a quantitative character. The input of additive genetic variance from mutation each generation, V_m, is assumed to be a constant independent of the amount of genetic variance already in the population. This can be justified by a detailed model of mutation in which at each locus there is a wide range of possible allelic effects with each allele mutating at the same rate with the same distribution of mutational changes in effect, although these parameters may differ between loci (Kimura 1965; Lande 1975). In a diploid randomly mating population, the expected rate of loss of heterozygosity, or additive genetic variance in a quantitative trait, due to random genetic drift in the absence of selection is $1/(2N_e)$ per generation, where N_e is the effective population size (Wright 1931, 1951; Latter and Novitski 1969). Measuring time, t, in generations, the dynamics of the expected value of the additive genetic variance, $\overline{V_g}$, under random genetic drift and mutation obey

$$\frac{d\overline{V_g}}{dt} = -\frac{\overline{V_g}}{2N_e} + V_m \qquad (1)$$

(Clayton and Robertson 1955; Lande 1979).

The effective population size may change with time. Here we assume that it is always a constant multiple of the actual population size (N_e/N = constant) and, starting from an

effective number of founders, $N_e(0)$, the population grows exponentially at the rate r per generation until reaching the final effective size, K_e. Thus the time in generations to reach the final size is $\tau = r^{-1}\ln(K_e/N_e(0))$ and the effective population size follows

$$N_e(t) = \begin{cases} N_e(0)e^{rt} & \text{for} \quad t < \tau \\ K_e & \text{for} \quad t \geq \tau \end{cases} \qquad (2)$$

To account for the age distribution of the founders, $N_e(0)$ can be approximated using standard (discrete generation) formulas involving sex-ratio and distributions of progeny numbers (Crow and Kimura 1970; Lande and Barrowclough 1987), starting with the initial total reproductive values of males and females (Fisher 1958; Pollard 1973) instead of the actual numbers of each sex.

For a population with overlapping generations, the generation time, T, is defined as the average age of mothers and fathers of newborn individuals in a population with a stable age distribution (assuming that the sex ratio of offspring is independent of parental age) (Leslie 1966; Hill 1979). With a constant life history (age-specific mortality and fecundity rates independent of time), T depends on the growth rate of the population, being smaller for populations that are more rapidly increasing (Leslie 1966). Because the change in generation time within species is likely to be small in comparison to the range in generation times among species managed by a single institution, and to simplify the analysis and facilitate comparison of the general results with those obtained by Soulé et al. (1986) we assume that T is approximately constant and ignore other complications caused by changes in age structure.

Fig. 1 displays results accounting for random genetic drift, but ignoring mutation (assuming $V_m = 0$). The upper right panel with $r = 0.5$ is nearly identical to Fig. 1 of Soulé et al. (1986) except that the axes have been reversed to emphasize that we wish to determine the final effective population size, K_e, necessary to preserve 90% of the

original additive genetic variance in the base population after 200 years, given T, $N_e(0)$ and r. An important feature of Fig. 1 is that when mutation is neglected the final effective population sizes needed to achieve this goal are extremely large for species with generation times of a few years or less. Note that when $r = 0.2$ and $N_e(0) = 20$ the management goal can not be attained for species with generation times less than 21.6 years.

[Fig.1 here]

Fig. 2 shows analogous results incorporating a typical level of mutation that has been observed in quantiatitve characters in a variety of organisms, $V_m = 10^{-3}V_e$ where V_e is the environmental variance in the character that would be expressed in a genetically uniform population (Lande 1975; Hill 1982; Lynch 1988a). We assume that the typical quantitative character in the base population has a heritability $h^2 = V_g(0)/[V_g(0) + V_e] = 0.5$ so that $V_g(0) = V_e$. Franklin (1980) apparently chose these same values for mutability and heritability when he suggested that in the absence of selection a population with $N_e = 500$ would maintain typical levels of additive genetic variance (Lande and Barrowclough 1987). It should therefore come as no surprise that, even for species with very short generation times, the value of K_e needed to achieve the management goal never exceeds 450 (or 90% of Franklin's number).

Comparison of Figs. 1 and 2 reveals that accounting for mutation allows the management goal to be met with a smaller number of founders. In the discrete generation model, Soulé et al. point out that $N_e(0)$ must be greater than 5 to preserve 90% of the genetic variability in the base population, since if $N_e(0) = 5$ then $1/(2N_e(0)) = 0.1$ of the genetic variability will be lost in the first generation. The accumulation of genetic variance by mutation over several generations can compensate for a loss of this magnitude, so that founder numbers smaller than previously proposed may be acceptable.

[Fig.2 here]

Immigration from the wild

Loss of genetic variance in a small captive population can be offset by immigration

from the wild, assuming that the wild population remains large enough to maintain its original genetic variability. For a given effective population size, immigration from the wild also has the effect of retarding random genetic drift in the mean phenotype of the captive population away from that in the wild population. In an equilibrium analysis of the "island model" Wright (1931, 1951) showed that immigration of a few individuals per generation will prevent substantial loss of genetic variability or differentiation by random genetic drift. Here we analyze a relatively simple model of the dynamics of additive genetic variance and random genetic drift in the mean phenotype of a small captive population subject to immigration from a large wild population.

The immigration rate from the wild to the captive population is defined as m, such that a proportion m of the captive population is replaced by wild individuals matched for sex and age. Let the wild population have additive genetic variance $V_g(0)$ in a quantitative character with mean phenotype $\bar{z}(0)$, which are assumed to remain constant. The variance in the probability distribution of the mean phenotype in the captive population caused by random genetic drift is denoted as $V_{\bar{z}} = E[(\bar{z}(t) - \bar{z}(0))^2]$. In this definition it is assumed that the mean phenotype is measured on a hypothetical large number of progeny; measurement of the actual population with effective size N_e would increase the expected variance in $\bar{z}(t)$ by an amount $(\overline{V_g} + V_e)/N_e$. The dynamics of the expected additive genetic variance within the captive population and the expected random genetic drift in its mean phenotype follow the coupled pair of equations

$$\frac{d\overline{V_g}}{dt} = -\frac{\overline{V_g}}{2N_e} + V_m + m\left[V_g(0) - \overline{V_g}\right] + \frac{m(1-m)}{2}V_{\bar{z}} \qquad (3)$$

$$\frac{dV_{\bar{z}}}{dt} = -2mV_{\bar{z}} + \frac{\overline{V_g}}{N_e} \qquad \text{assuming } m << 1.0 \qquad (4)$$

(Lande 1979; Lynch 1988b). The last two terms in equation (3) correspond respectively to

the genetic variance carried by the immigrants and the genetic variance that is produced by hybridization between populations. For simplicity we assume that N_e is constant and equal to the size of of the founder population. We also assume that immigration occurs at a small constant rate, $m << 1.0$.

Fig. 3 (*left*) shows that with typical levels of mutation even one effective migrant every few generations ($N_e m$ = 1/4, 1/2, or 1) substantially reduces the effective population size necessary to achieve the management goal. The actual number of immigrants, Nm, differs from the effective number of immigrants. $N_e m$ can be estimated from the expected reproductive value of the immigrants times N_e/N for the captive population.

Fig. 3 (*right*) depicts the amount of random genetic drift in the mean phenotype for populations managed to maintain 90% of the original genetic variance after 200 years (as shown in Fig. 3 *left*). The mean phenotype in the population is expected to drift less than one phenotypic standard deviation in 200 years, except for populations with generation times less than 0.5 year in the absence of immigration. When $N_e m$ is in the range of 1/4 to 1, more phenotypic differentiation is expected to occur than in the absence of immigration, unless the generation time is less than 1 or 2 years. This result, which at first seems counterintuitive, occurs because these immigration rates allow the management goal to be met with smaller effective population sizes, which increases the rate of random genetic drift in the mean phenotype. With $N_e m > 2$, there is expected to be less phenotypic differentiation than in the absence of immigration because the stabilizing influence of immigration on the mean phenotype is stronger than the random genetic drift caused by reduced N_e.

[Fig. 3 here]

Selection in the captive environment

Newly established captive populations often experience substantial selection to adapt to the captive environment. This includes novel physical conditions such as confinement, and new social and biotic factors such as isolation or crowding, and exposure to an altered set

of pathogens. There may be additional artificial selection by the managers (consciously or unconsciously) for docility and high reproductive rate, especially during the early history of the population. In addition, relaxation of natural selection may result in the gradual deterioration of some characters subject to directional mutation, and maintained by mutation-selection balance in wild populations, especially traits most closely related to fitness in the wild, e.g. sensory acuity, agility and cognitive function. Higher animal species may also experience a loss of culturally transmitted information during a period of a generation or more in captivity.

The effect of selection in the captive environment on the additive genetic variance of a particular trait can be modelled crudely by the loss of a constant proportion s per generation, so that equation (1) is modified to

$$\frac{d\overline{V_g}}{dt} = -\left(\frac{1}{2N_e} + s\right)\overline{V_g} + V_m \quad . \qquad (5)$$

Fig. 4 (*left*) reveals that with typical rates of mutation, if s is as small as 1%, even an infinitely large population will not maintain 90% of the original genetic variance for 200 years, unless the generation time of the species is rather long. It may therefore be impossible to meet the management goal for characters under appreciable selection in captivity. Instead of causing dispair, this conclusion can be turned around, in the manner of Fig. 4 (*right*). For species with short generation times, populations with a moderate effective size will maintain nearly as much genetic variance in selected characters as an infinitely large population.

Deleterious or undesirable evolution in captive populations, caused by adaptation to captivity or by mutation and random genetic drift, can be counteracted by immigration from the wild, or by artificial selection imposed by managers. To have much effect in this context, the rate of immigration would have to be comparable to the strength of selection

($m \geq s$). The imposition of artificial selection to counteract natural selection in captivity would help to prevent change in the mean phenotype, but may also increase the rate of loss of additive genetic variance. Another way of reducing evolutionary changes in a captive population is by increasing generation time and equalizing progeny numbers. Any required artificial selection should be exerted within progeny groups, with readjustment to equal size after selection (Lande and Barrowclough 1987).

[Fig. 4 here]

Population subdivision

Subdivision of a population and random genetic drift within the subpopulations converts the original genetic variation within the base population into genetic variation between subpopulations. Population subdivision also allows genetic variation between populations to accumulate by random genetic drift and fixation of new mutations. Once alternative alleles at a locus are fixed in different subpopulations, this component of genetic variability is permanently maintained and can not be lost as long as the subpopulations persist. Splitting a population into separate subpopulations with no gene flow or migration among them is therefore a powerful way of maintaining genetic variability, even though the total population size may be small.

Consider a panmictic population with an effective population size N_e that is divided at time 0 into n separate subpopulations, each with constant effective size N_e/n. The additive genetic variance maintained by this population structure after t generations can be measured by the amount that would exist if the all subpopulations were randomly mated and allowed to attain linkage equilibrium (e.g. after several generations at large population size). Since purely additive genetic variance within populations is expected to double when converted by random genetic drift to variation among populations (Wright 1951) the total additive genetic variance in the population after panmixia, V_{gP}, is expected to be

$$\overline{V_{gP}}(t) = \overline{V_g}(t) + \tfrac{1}{2}(1 - 1/n)V_{\overline{z}}(t) \qquad (6)$$

where $\overline{V_g}(t)$ and $V_{\bar{z}}(t)$ are respectively the expected genetic variance within subpopulations and the expected differentiation among subpopulations, as defined above eqns. (3) and (4).

The preservation of heterozygosity or additive genetic variance in a subdivided population is most easily illustrated when there is no mutation, migration or selection. Although smaller subpopulations lose genetic variance faster, Fig. 5 shows that splitting a population of a given total size into more subpopulations is expected to result in the preservation of more genetic variance. After a few times N_e/n generations, the amount of additive genetic variance preserved among n subpopulations approaches $(1 - 1/n)V_g(0)$.

[Fig. 5 here]

With mutation, but no migration or selection, the subpopulations will continue to differentiate, and, after many generations have elapsed, the total genetic variance as measured by eqn. (6) will actually exceed that originally contained in the base population. Fig. 6 (*left*) gives the total population size, N_e, needed to maintain 90% of the initial genetic variance in a typical quantitative character after 200 years, with various numbers of subpopulations. The curves for $n \geq 2$ are truncated because species with generation times less than a few years are always expected to maintain *more* than 90% of the original genetic variance, regardless of the total population size, because of the accumulation of new mutations among populations.

Subdivision can also help to counteract the erosion of genetic variability by selection in the captive environment, if subpopulations are small enough so that random genetic drift and fixation of alternate alleles in different subpopulations occurs faster than selection. For example, Fig. 6 (*right*) depicts the simple case where directional selection operates with the same intensity on all subpopulations, regardless of their mean phenotype (e.g. due to unconscious artificial selection for tameness). It can be seen that for species with intermediate generation times, splitting the population into many very small subpopulations makes the management goal attainable, and with feasible total population sizes. Stabilizing

selection toward the same phenotype in all subpopulations would retard their differentiation and reduce the impact of subdivision, whereas diversifying selection toward different phenotypes in different subpopulations would accelerate their differentiation and enhance the influence of subdivision in comparison to that shown in Fig. 6 (*right*).

[Fig. 6 here]

Summary and Discussion

Breeding plans for captive populations should be designed to meet a specific goal. Possible goals range from the establishment of a permanent captive population for public display in zoos or arboreta, to captive breeding for later release into the wild (Frankham et al. 1986; Foose et al. 1986). The present paper concerns captive breeding for later release into the wild. For many species, especially large mammals and birds, or species with specialized habitat requirements, continued habitat alteration (directly or indirectly by human exploitation) will cause extinction or near extinction in the wild, necessitating a period of captive propagation to produce stock for later release into natural or restored areas. Soulé et al. (1986) suggested the management goal of maintaining 90% of the initial heterozygosity for 200 years. We derived an analytical framework for the development of breeding plans designed to meet this goal for additive genetic variance in typical quantitative characters. Results are presented in the figures. General analytical formulas in the Appendix allow construction of breeding plans to meet other goals, such as maintanence of 75% of the original genetic variability for 100 years.

Building on the model of Soulé et al. (1986) which includes the number of founders, exponential growth of the population to its final size, and random genetic drift, the present results demonstrate that the management goal can be achieved with smaller population sizes if account is taken of mutation in typical quantitative traits. This is especially important for species with short generation times, as can be seen from comparison of Figs. 1 and 2.

Immigration from the wild of one effective individual every few generations would also permit substantial reduction in the size of the managed population necessary to meet the goal (Fig. 3), but this option is not possible if the wild population is extinct, and it may not be desirable if the wild population has been severly reduced in size for several generations so that it is highly inbred and depauperate of genetic variability.

These models analyze the dynamics of genetic variability, assuming that in the captive environment there is no selection on most characters. However, for some traits, such as tameness, and fecundity, natural or artificial selection for adaptation to captivity may occur. With appreciable selection in the captive environment, the management goal can not be met using a single panmictic population, except for species with rather long generation times. In this situation, a population with an effective size of a few hundred individual can maintain nearly as much genetic variability as an indefinitely large population, as shown in Fig. 4.

Breeding plans for closely managed populations often have a single (nearly) panmictic population with an effective size large enough to avoid severe inbreeding depression and to maintain substantial amounts of selectively neutral heterozygosity or additive genetic variance in quantitative traits for long periods of time (Franklin 1980; Foose et al. 1986; Soulé et al. 1986). Random exchange of one effective immigrant every few generations between subdivisions of a population renders it nearly panmictic with respect to selectively neutral variation (Wright 1951; Foose et al. 1986). Most of the deleterious effects of inbreeding depression can be avoided if the subpopulations have effective size greater than a few dozen individuals (Lande and Barrowclough 1987). This degree of subdivision also has the advantage of reducing the chance of catastrophic extinction (e.g. by epidemics) and regionalizing logistical problems including transportation costs (Foose et al.1986).

Complete subdivision of a population acts to permanently maintain genetic variability between subpopulations rather than within them. Subdivision of a population into noninterbreeding units may be appropriate if the management goal can not be met with a

single randomly mating population because of space limitations (Figs. 5 and 6 *left*). Extreme subdivision into numerous very small subpopulations may be the only method of maintaining a high proportion of the original genetic variation for characters that are under appreciable selection for adaptation to captivity. However, the subpopulations should not be so small that they experience severe inbreeding depression. Choice of the degree of subdivision (e.g., Fig. 6 *right*) should be based on consideration of the intensity of selection and the magnitude of inbreeding depression. Stronger selection requires more subdivision, but larger subpopulation size allows selection to more efficiently counteract inbreeding depression by eliminating deleterious recessive mutations when they become homozygous.

In addition to the goal of maintaining genetic variability, breeding plans should also limit evolution of mean phenotype in the captive population by random genetic drift or selection in the captive environment. The Appendix and Fig. 3 show that for the breeding plans described above, random genetic drift in the mean phenotype is not expected to be substantial, unless the generation time of the species is much less than one year (i.e., on the order of one month). Aside from reducing the intensity of selection (by equalizing family sizes, maximizing generation time, and eliminating conscious selection) or continually introducing immigrants from the wild, extreme population subdivision may be the most powerful method of reducing the influence of selection in the captive environment. To counteract deleterious mutations or undesirable evolutionary changes in quantitative traits, Lande and Barrowclough (1987) recommend artificial selection within families, maintaining equal family sizes after selection.

When a captive population is released into a natural or restored area, the initial founders must reproduce suffiently fast for the population to grow and become established at a size large enough to avoid extinction from ecological and genetic factors. The number of individuals released should be sufficiently large to prevent substantial inbreeding and loss of genetic variability, and to overcome Allee effects such as the difficulty of finding a mate

in a sparse population. The period of captive propagation should encompass as few generations as possible, to minimize loss of genetic variation, cultural information and domestication effects. The environment of release should be similar to the original natural habitat to reduce the difficulty of adaptation. In many cases, multiple releases at various localities will be necessary for successful establishment in the wild (Griffith et al. 1989).

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Appendix

Random genetic drift and mutation. Eqn. (1) is first-order and linear, with nonconstant coefficient $1/(2N_e(t))$ given by eqn. (2). It can be solved using an integrating factor. From the solution, given $V_g(0)$, $N_e(0)$, r and T, we wish to derive the value of K_e that will satisfy the management goal. Thus we require that the final effective population size has been reached, $t \geq \tau$, and that after $t = 200/T$ generations an expected proportion p (here $p = 0.9$) of the initial additive genetic variance is maintained, $\overline{V_g}(200/T) = pV_g(0)$. The solution of eqn. (1) at $t = \tau$ is

$$\overline{V_g}(\tau) = I(\tau)\left[V_g(0) + V_m \int_0^{\tau} [I(u)]^{-1} du\right] \tag{A1}$$

where the integrating factor is

$$I(\tau) = \exp\left\{ -\frac{1 - e^{-r\tau}}{2N_e(0)r} \right\} \tag{A2}$$

and $\tau = r^{-1}\ln(K_e/N_e(0))$. For $t \geq \tau$, the solution is

$$\overline{V_g}(t) = 2K_eV_m + \left[\overline{V_g}(\tau) - 2K_eV_m\right]\exp\left\{ -\frac{t - \tau}{2K_e} \right\} \tag{A3}$$

Although it is not possible to obtain an explicit expression for K_e from these formulas, t can be expressed in terms of K_e as

$$t = \tau + 2K_e \ln\left\{ \frac{\overline{V_g}(\tau) - 2K_eV_m}{pV_g(0) - 2K_eV_m} \right\} \tag{A4}$$

in which $\overline{V_g}(\tau)$ is given by (A1). Generation times are then obtained from $T = 200/t$.

In the absence of mutation ($V_m = 0$) the term in brackets in the denominator of (A4) becomes simply $I(\tau)/p$ as was used to construct Fig. 1. With mutation it is convenient to divide numerator and denominator in the bracketed term by $V_g(0)$, setting $V_m/V_g(0) =$

$(V_m/V_e)(1 - h^2)/h^2$ in which h^2 is the heritability of the character in the base population (see text). To construct Fig. 2, the integral in (A1) was evaluated by substituting $y = \alpha e^{-ru}$ with $\alpha = [2N_e(0)r]^{-1}$,

$$\int_0^{\tau} [I(u)]^{-1} du = r^{-1} e^{\alpha} [E_1(\alpha e^{-r\tau}) - E_1(\alpha)] \qquad (A5)$$

where $E_1(x) = \int_x^{\infty} y^{-1} e^{-y} dy$ is the exponential integral. In the range $0 \le x \le 1$ (if $r > 0$ this requires that $2N_e(0)r \ge 1$), the exponenital integral can be approximated with an error less than 2×10^{-7} by the function (Abramowitz and Stegun 1972)

$$E_1(x) = \ln x + a_0 + a_1 x + a_2 x^2 + a_3 x^3 + a_4 x^4 + a_5 x^5 \qquad (A6)$$

with

$a_0 = -0.57721566$	$a_3 = 0.05519968$
$a_1 = 0.99999193$	$a_4 = -0.00976004$
$a_2 = -0.24994055$	$a_5 = 0.00107857$

Immigration from the wild. Eqns. (3) and (4) constitute a coupled pair with constant coefficients, which can be solved by finding the eigenvalues and eigenvectors of the system. Since we have assumed that $m << 1$, the last coefficient in eqn. (3) can be approximated as $m(1 - m)/2 \equiv m/2$. We must analyze separately the cases of positive migration rate and no migration since the solution changes discontinuously as m approaches 0.

For $m > 0$, the equilibrium values of the variables are

$$\overline{V_g}(\infty) = 4N_e[V_m + mV_g(0)]/(4N_e m + 1) \qquad (A7)$$

$$V_{\bar{z}}(\infty) = \overline{V_g}(\infty)/(2N_e m) \quad . \qquad (A8)$$

Defining $\delta(t) = \overline{V_g}(t) - \overline{V_g}(\infty)$ and $\varepsilon(t) = V_{\bar{z}}(t) - V_{\bar{z}}(\infty)$ eqns. (3) and (4) become

$$\frac{d}{dt}\begin{pmatrix}\delta\\ \varepsilon\end{pmatrix} = \begin{pmatrix}-m - 1/(2N_e) & m/2\\ 1/N_e & -2m\end{pmatrix}\begin{pmatrix}\delta\\ \varepsilon\end{pmatrix} \tag{A9}$$

The eigenvalues of the matrix in (A8) are $-m$ and $\lambda = -1/(2N_e) - 2m$, with corresponding eigenvectors in transposed form $(N_e m, 1)$ and $(-1/2, 1)$. Then

$$\overline{V_g}(t) = \overline{V_g}(\infty) + c_1 N_e m e^{-mt} - (c_2/2)e^{\lambda t} \tag{A10}$$

$$V_{\bar{z}}(t) = V_{\bar{z}}(\infty) + c_1 e^{-mt} + c_2 e^{\lambda t} \tag{A11}$$

where, using $V_{\bar{z}}(0) = 0$ and (A8),

$$c_1 = [\overline{V_g}(\infty) - 2\overline{V_g}(0)]/(2N_e m + 1)$$

$$c_2 = 2[\overline{V_g}(0) - (1 + 1/(4N_e m))\overline{V_g}(\infty)]/(2N_e m + 1) \quad .$$

Setting $\overline{V_g}(t) = pV_g(0)$ in eqn. (A10), and dividing all genetic variances by $V_g(0)$ as after (A4), Newton's method of iteration was used to find numerical values of t for given values of N_e, $N_e m$, $\dot{V}_m/V_e$ and the initial heritability h^2. Numerical values of t were converted to generation times using $T = 200/t$ to plot the solid curves in Fig. 3a, and they were also substituted into (A11) to construct the solid curves in Fig. 3b.

For $m = 0$, the solutions of eqns. (3) and (4) are

$$\overline{V_g}(t) = 2N_e V_m + [V_g(0) - 2N_e V_m]e^{-t/(2N_e)} \tag{A12}$$

$$V_{\bar{z}}(t) = 2[V_g(0) - 2N_e V_m][1 - e^{-t/(2N_e)}] + 2tV_m \quad . \tag{A13}$$

(Lande 1980). These formulas were used to plot the dashed curves in Figs. 3a and 3b, proceeding as with (A10) and (A11), except that an analytical expression for t can be easily obtained from (A12).

Selection in captivity. Eqn. (5) is linear with constant coefficients. Setting $\lambda = 1/(2N_e) + s$ the solution is

$$\overline{V_g}(t) = \lambda^{-1}V_m + [V_g(0) - \lambda^{-1}V_m]e^{-\lambda t} . \qquad \text{(A14)}$$

Setting $\overline{V_g}(t) = pV_g(0)$ and solving for t yields

$$t = \lambda^{-1} \ln\left\{ \frac{V_g(0) - V_m/\lambda}{pV_g(0) - V_m/\lambda} \right\} \qquad \text{(A15)}$$

Again $T = 200/t$ and the variances in the bracketed term can expressed in units of $V_g(0)$ as after eqn. (A4). Eqns. (A15) and (A14) were used respectively to produce the left and right sides of Fig. 4.

Population subdivision. From eqn. (6), using (A12) and (A13) with N_e divided by n, we find that with no mutation, and no selection or migration

$$\overline{V_{gP}}(t) = V_g(0)[1 - (1 - e^{-nt/(2N_e)})/n] \qquad \text{(A16)}$$

which was used to construct Fig. 5. With a constant intensity of directional selection on each subpopulation, regardless of its mean phenotype, eqn. (5) with N_e divided by n describes the dynamics of $\overline{V_g}$, and the expected differentiation among subpopulations is given by $dV_{\bar{z}}/dt = n\overline{V_g}/N_e$. The expected total genetic variance after panmixia in generation t, with selection and mutation, but no migration, is then

$$\overline{V_{gP}}(t) = [V_g(0) - V_m/\lambda][c/\lambda + (1 - c/\lambda)e^{-\lambda t}] + (1 + ct)V_m/\lambda \qquad \text{(A17)}$$

where $\lambda = n/(2N_e) + s$ and $c = (n - 1)/(2N_e)$. Setting $\overline{V_{gP}}(t)/V_g(0) = 0.9$, this equation was evaluated as above for a typical character with $h^2 = 0.5$ and $V_m/V_e = 0.001$. Newton's method was employed to obtain numerical solutions for t which were converted to generation times using $T = 200/t$ for the construction of Fig. 6.

Random genetic drift in the mean phenotype. For completely additive genetic variance Wright (1951) showed that random drift in the mean phenotype of a single population is expected to cause a squared deviation between the initial and final mean phenotypes of $2V_g(0)$ based on fixation of the original genetic variation. Random genetic drift and fixation of new mutations are expected to add a quantity less than $2tV_m$, regardless of $N_e(t)$ (Lande 1980; eqn. A13). Defining $v_{\bar{z}}(t) = V_{\bar{z}}(t)/[V_g(0) + V_e]$, then

$$v_{\bar{z}}(t) < 2h^2 + 2t(V_m/V_e)(1 - h^2) \quad . \qquad \text{(A18)}$$

At $t = 200/T$, the mean phenotype of a typical character with heritability $h^2 = 0.5$ and $V_m/V_e = 0.001$ is not expected to drift more than one phenotypic standard deviation because of fixation of genetic variation in the base population, and less than an additional $1/(5T)$ phenotypic standard deviations based on new mutations. Thus unless $T << 1$, random genetic drift in the mean phenotype is not likely to be substantial in breeding plans for a single population carried out on a timescale of 200 years.

The same conclusion holds with population subdivision, regardless of the sizes of the subpopulations or the migration rates between them. Let the ith subpopulation have mean phenotype $\bar{z}_i$ (measured in a large number of offspring), additive genetic variance V_{gi} and effective size N_{ei}. The ratio of actual to effective size is assumed to be the same in all subpopulations, so that the total effective size in the absence of subdivision would be $N_e = \Sigma N_{ei}$. The grand mean phenotype and the weighted average genetic variance within subpopulations are

$$\bar{z} = \sum N_{ei}\bar{z}_i / N_e \quad \text{and} \quad \overline{V_g} = \sum N_{ei}V_{gi} / N_e \tag{A19}$$

The increased variance in the probability distribution of $\bar{z}$ due to one generation of random genetic drift is

$$\mathrm{Var}_{\mathrm{drift}}[\bar{z}] = \sum (N_{ei}/N_e)^2 V_{gi}/N_{ei} = \overline{V_g}/N_e \ . \tag{A20}$$

This result is not influenced by migration among subpopulations, provided that individuals do not incur reduced fitness during migration, because with purely additive genetic variance migration does not alter $\bar{z}$. Thus random genetic drift in $\bar{z}$ occurs at the same rate as if the population were panmictic with additive genetic variance $\overline{V_g}$. Because population subdivision is expected to decrease the additive genetic variance within subpopulations (Wright 1951; Lynch 1988b), the rate of genetic drift in the grand mean phenotype of a subdivided population must be less than that for a single panmictic population with the same total effective size, analyzed in (A18).

Figure Captions

Fig. 1. Final effective size of a captive population, K_e, necessary to expect 90% of the original heterozygosity, or additive genetic variance in quantitative characters, in the base (wild) population after 200 years, as a function of the generation time, for various values of the effective number of founders, $N_e(0)$, and population growth rate per generation, r. From eqns. (1) and (2), assuming no mutation.

Fig. 2. The same as Fig. 1, but for a typical quantitative character with additive genetic variance created by mutation at the rate $V_m/V_e = 0.001$ per generation, and a heritability in the base (wild) population of $h^2 = 0.5$.

Fig. 3. *Left.*-- Effective population size, N_e, needed to expect 90% of the original additive genetic variance after 200 years, as a function of the generation time, for various values of the effective number of immigrants per generation from the wild, $N_e m$, assuming $V_m/V_e = 0.001$ and $h^2 = 0.5$. *Right.*-- Expected amount of random genetic drift in the mean phenotype, in units of phenotypic standard deviations in the wild population, as a function of the generation time, when N_e is kept for 200 years at the size given in the left graph. From eqns. (3) and (4).

Fig. 4. *Left.*-- Effective size of a captive population, N_e, necessary to expect 90% of the initial additive genetic variance after 200 years, as a function of the generation time, for various values of the rate of selective loss of genetic variance, s. *Right.*-- Expected proportion of additive genetic variance maintained after 200 years as a function of N_e, for various values of the generation time, assuming $s = 0.01$. From eqn. (5).

Fig. 5. Expected proportion of original heterozygosity or additive genetic variance maintained as a function of time, for various numbers of subpopulations, n. Time is scaled in units of $2N_e$, where N_e is the total effective size if the population were panmictic. There is no mutation or selection, and no gene flow or migration among subpopulations. From eqn. (6).

Fig. 6. *Left.*-- Total population size, N_e, needed to maintain 90% of the initial additive genetic variance after 200 years, as a function of the generation time, for various numbers of subpopulations, n. Evaluated for a character with $V_m/V_e = 0.001$ and $h^2 = 0.5$, but with no selection and no migration among subpopulations. *Right.*-- Same as the left side, but there is selection, $s = 0.01$ and no mutation, $V_m = 0$. From eqns. (5) and (6).

Fig. 1

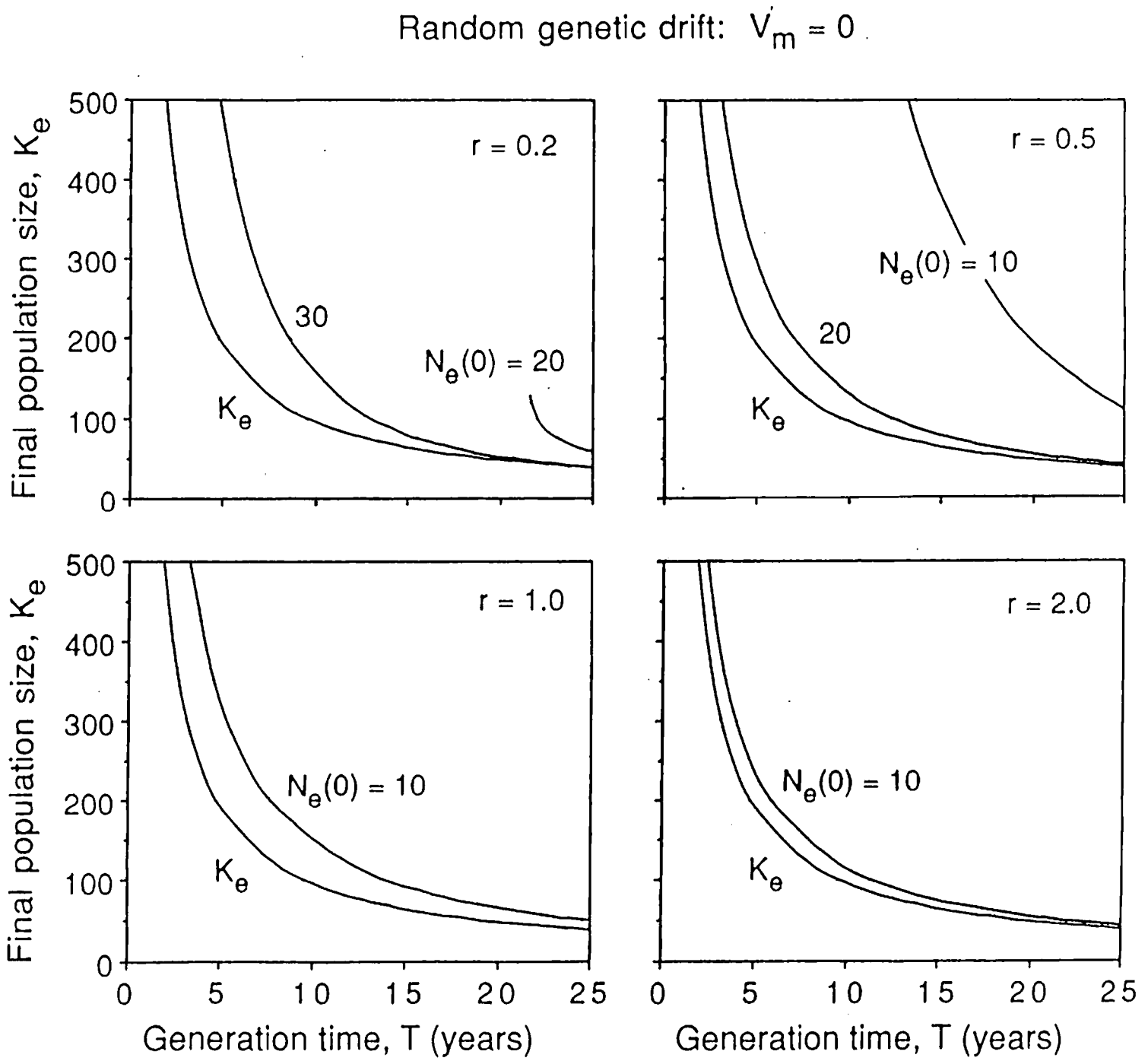

Random genetic drift: $V_m = 0$
Final population size, K_e
500
400
300
200
100
0
r = 0.2
30
$N_e(0) = 20$
K_e
r = 0.5
$N_e(0) = 10$
20
K_e
r = 1.0
$N_e(0) = 10$
K_e
r = 2.0
$N_e(0) = 10$
K_e
0 5 10 15 20 25
Generation time, T (years)

Fig. 2

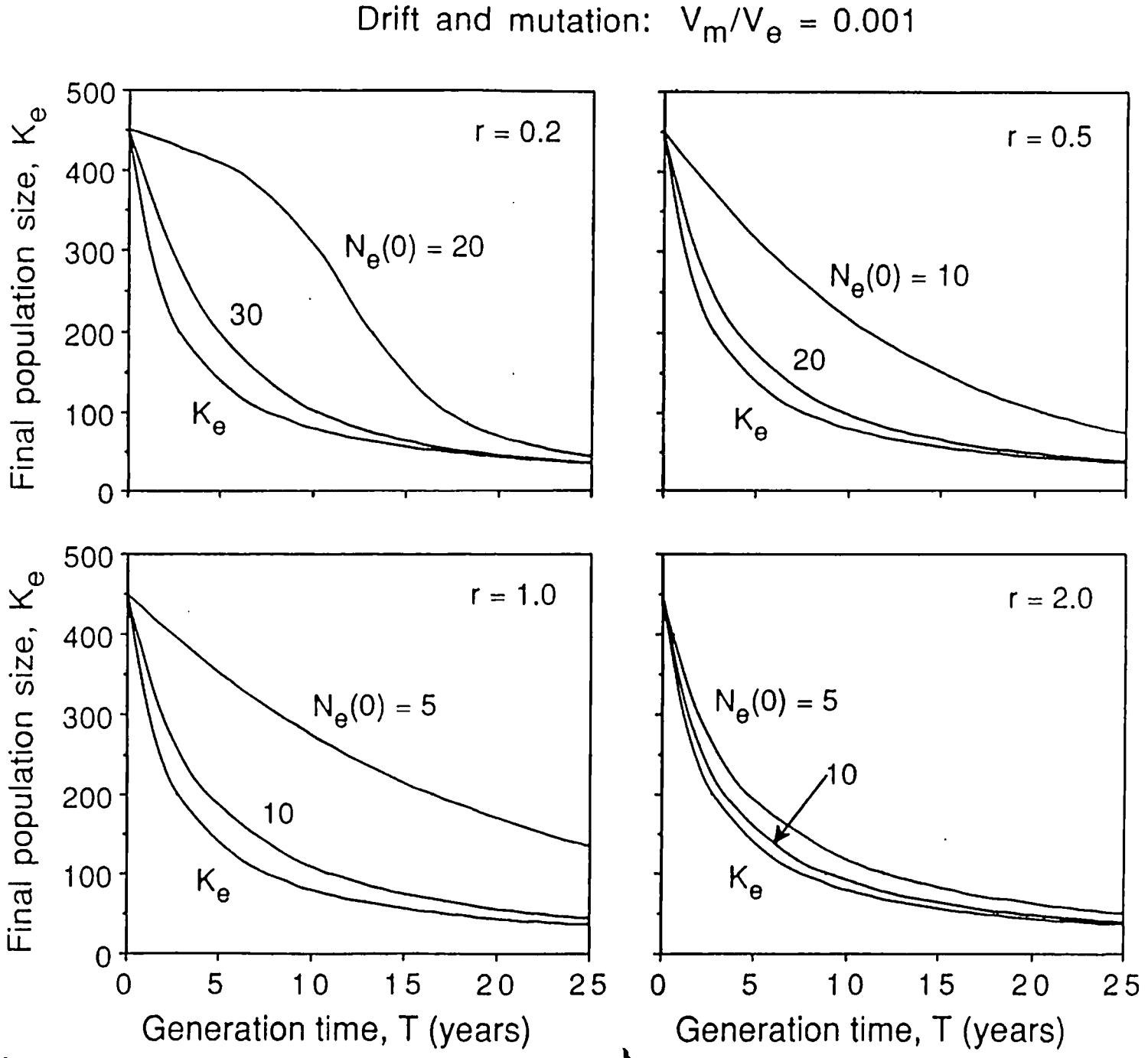
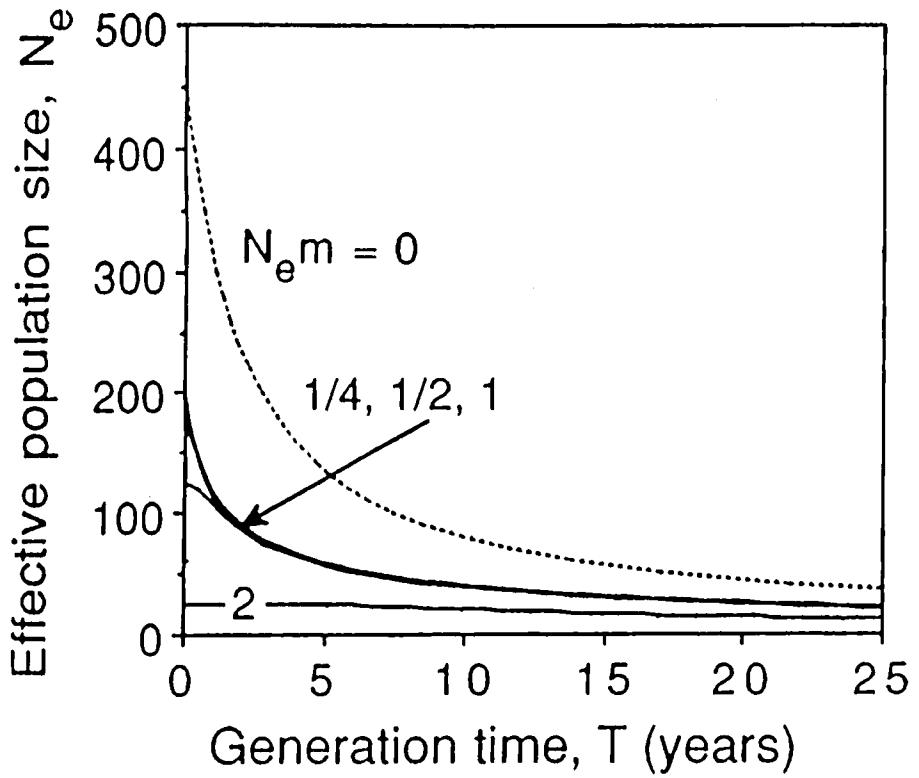

Drift and mutation: V_m/V_e = 0.001
Final population size, K_e
500
400
300
200
100
0
r = 0.2
$N_e(0)$ = 20
30
K_e
r = 0.5
$N_e(0)$ = 10
20
K_e
r = 1.0
$N_e(0)$ = 5
10
K_e
r = 2.0
$N_e(0)$ = 5
10
K_e
0
5
10
15
20
25
Generation time, T (years)

Fig. 3


Effective population size, N_e
500
400
300
200
100
0
$N_em = 0$
1/4, 1/2, 1
2
0
5
10
15
20
25
Generation time, T (years)

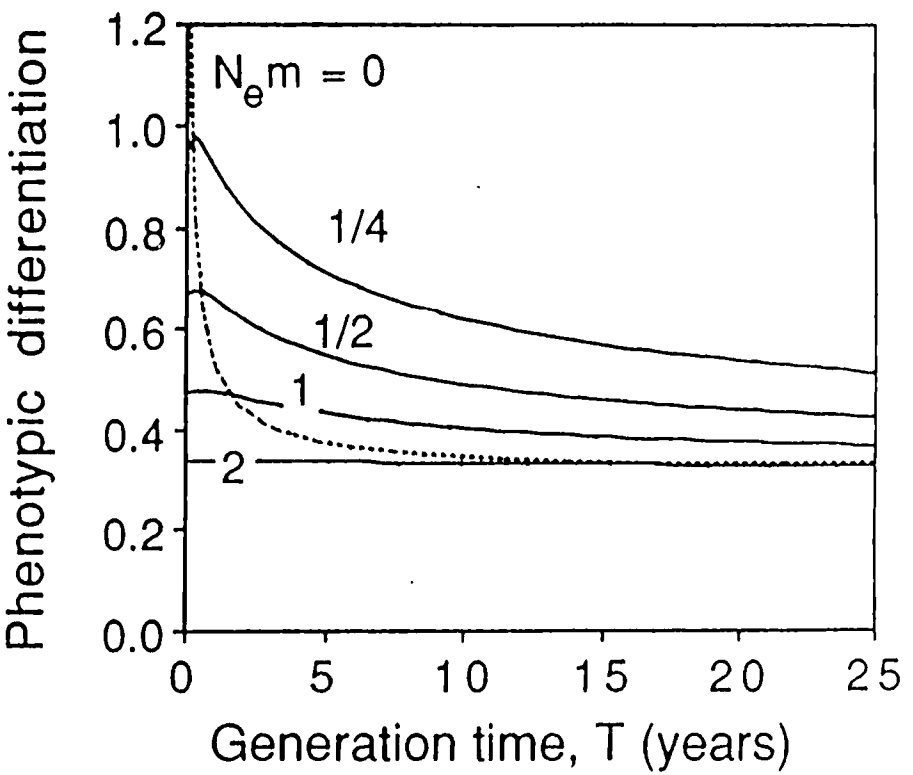
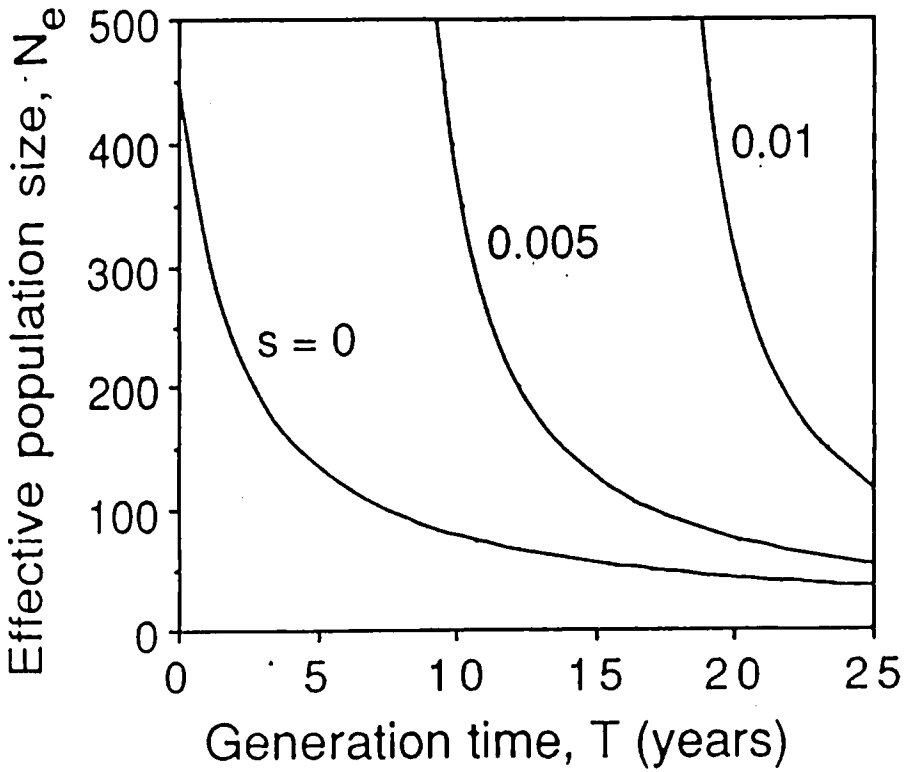

Phenotypic differentiation
1.2
1.0
0.8
0.6
0.4
0.2
0.0
$N_em = 0$
1/4
1/2
1
2
0
5
10
15
20
25
Generation time, T (years)

Fig. 4


Effective population size, N_e
500
400
300
200
100
0
0
5
10
15
20
25
Generation time, T (years)
s = 0
0.005
0.01

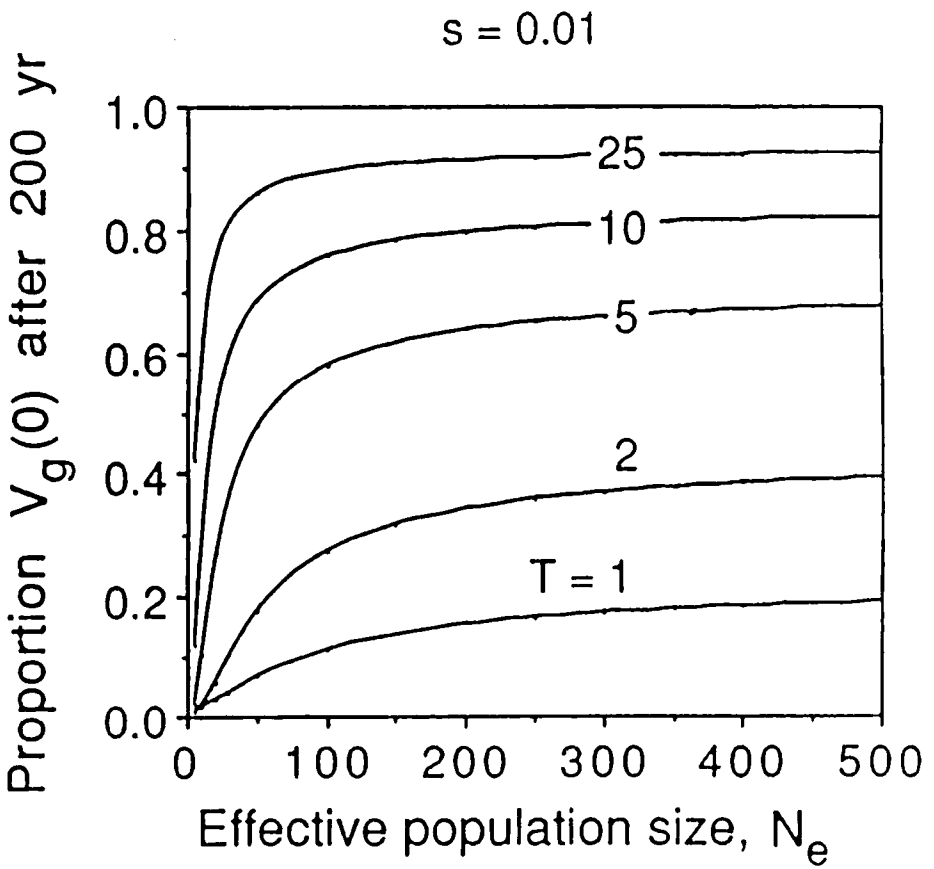

s = 0.01
Proportion $V_g(0)$ after 200 yr
1.0
0.8
0.6
0.4
0.2
0.0
0
100
200
300
400
500
Effective population size, N_e
25
10
5
2
T = 1

Fig. 5

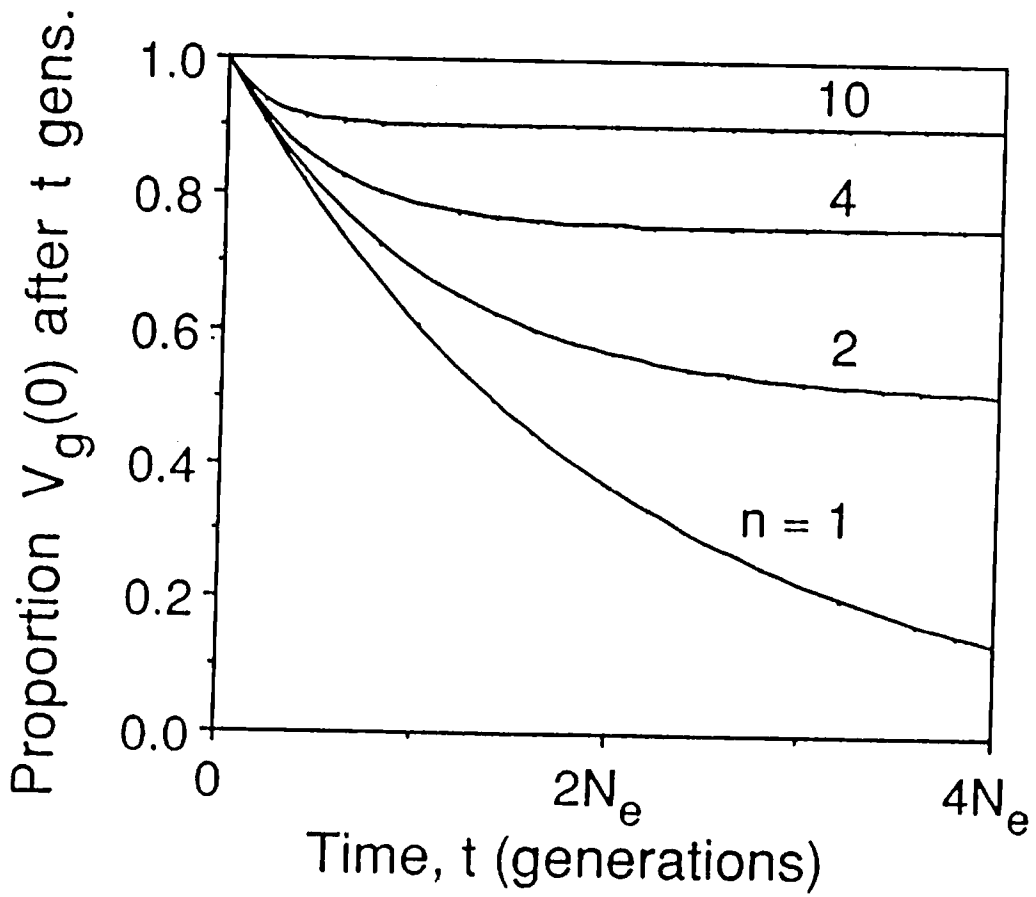
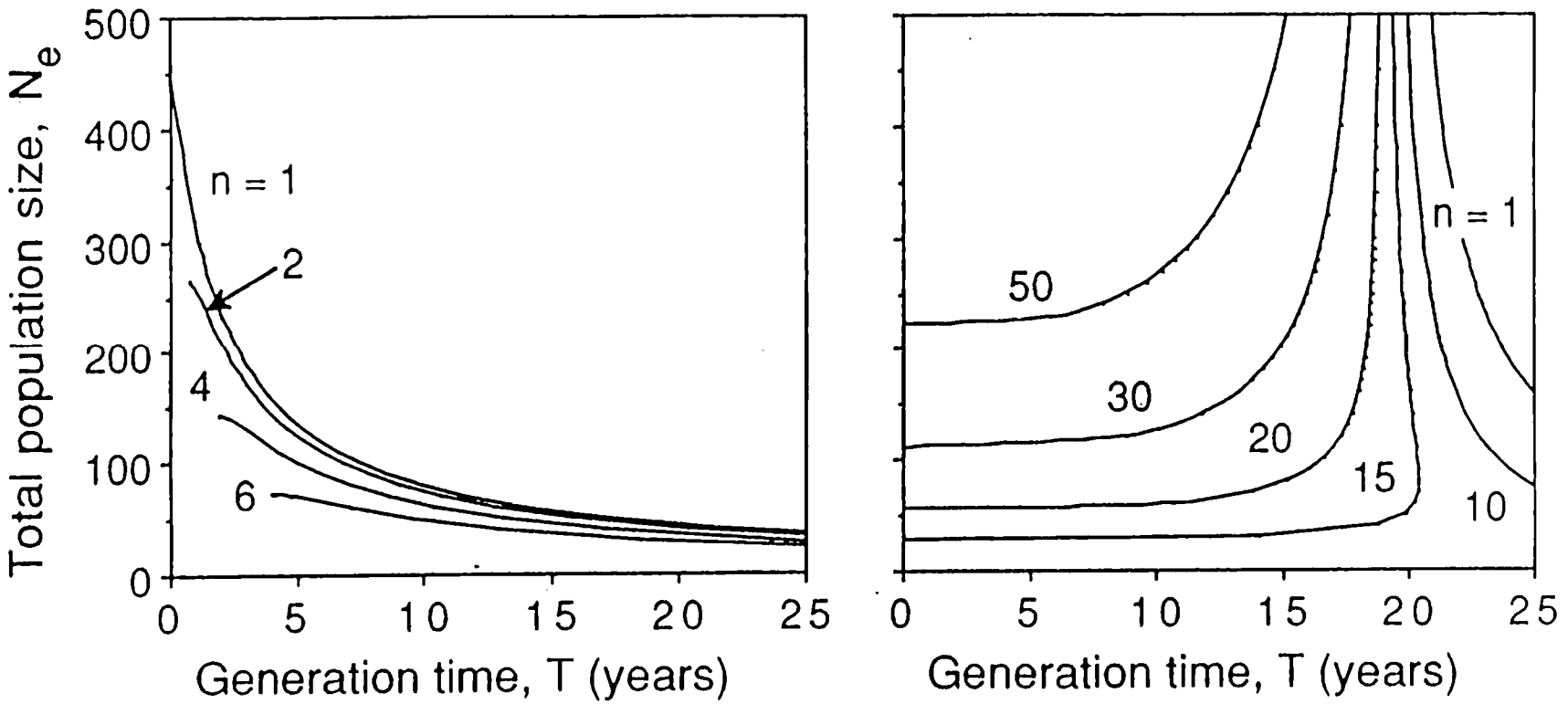

Proportion $V_g(0)$ after t gens.
1.0
0.8
0.6
0.4
0.2
0.0
0
$2N_e$
$4N_e$
Time, t (generations)
10
4
2
n = 1

Fig. 6


Total population size, N_e
500
400
300
200
100
0
n = 1
2
4
6
0
5
10
15
20
25
Generation time, T (years)
50
30
20
15
10
n = 1
0
5
10
15
20
25
Generation time, T (years)