GENETICS, MINIMUM POPULATION SIZE, AND THE ISLAND PRESERVE

Christine Schonewald-Cox

ABSTRACT

Small populations are often extinction-prone because they are too small demographically or because they contain too little genetic diversity to adapt to change or to give rise to new species. In the genetic context, minimum effective population size may be defined as that level in which 90% of genetic diversity is retained over evolutionary time. Genetic diversity may be maintained within populations or among populations of a species. In outbreeding species, extinction can be precipitated by loss or skewing of allele frequency through genetic drift and by loss of alleles through small population sampling effects. Inbreeding depression (including increasing genetic load) results in lowered survival and ultimately population decrease. In typically inbreeding and polyploid species, where genetic variability is stored among populations, loss of populations is an important step in the process of extinction. Lack of genetic variation within populations reduces ability to adapt to the catastrophic changes often brought about by man, and also predisposes populations of these species to extinction. Hawaiian endemics resulted from colonization by small groups or single founders and many of these may have been subjected to repeated bottlenecks adapting them to small population size and inbreeding. Management approaches to alter survival probabilities include increasing gene flow among captive individuals and populations to enhance genetic diversity, and mate manipulation to adapt small captive populations to inbreeding and minimize inbreeding depression. When management increases adaptation to inbreeding, efforts to also increase population size rapidly will decrease the probability of inbreeding depression and help reduce loss of rare alleles remaining in a population. Hawaiian species that are present in moderate numbers but are threatened or that appear to have recovery potential from smaller population size should be subjected to the

following analysis: 1) determine population isolation and adaptation to inbreeding; 2) if population is so adapted, separate and isolate small founder populations throughout habitat pockets; 3) if populations are not adapted to inbreeding, establish several small captive populations for inbreeding and eventual reintroduction; and 4) consider use of controlled backcrossing to regenerate variability and plan for eventual reintroduction.

INTRODUCTION

During the last few thousand years, the Hawaiian Islands have experienced rapid and large scale extinctions. Recently, lands have been set aside in preserves and parks to protect habitats and populations of endemic species, yet population declines continue. The number of species able to survive will be determined, at least indirectly, by the shape of parks and reserves, their numbers, sizes, and surrounding land uses, and the distances between reserves. Even if ecosystem deterioration ceases, the total capacity of the Islands for native species will obviously be far less than was historically possible before colonization by humans.

Habitat loss and continued presence of alien species populations greatly accentuate the protected habitat and island isolation effects that characterize Hawaiian endemics. Thus, declines continue regardless of the effectiveness with which boundaries of parks and preserves are protected. Trends to extinction can be countered through habitat accession and restoration, innovative defenses of preserve boundaries, and innovative management of declining populations. While the odds are strongly against success, there are new and promising developments in habitat and population restoration techniques that are worth pursuing.

In addition to its habitat, each species has basic requirements for reproduction and evolutionary survival that are strongly influenced by population numbers, sizes, and gene exchange. While some characteristics predispose some species to difficult times in rapidly changing environments, others predispose more flexible species to colonize under changing environmental conditions. When populations are small and isolated, their basic predispositions for colonizing or for extinction are accentuated.

Genetic characteristics of species determine how they will respond to preserve design and management. Design and management will determine what levels of isolation and dispersion of genetic diversity will exist within the protected area for any given species

(Soule and Wilcox 1980). Inevitably, when species distributions and movements are restricted to isolated protected areas, natural patterns of gene exchange and rates of evolution are affected. Restrictions on distribution and movement are often imposed by factors not related to natural events. For example, preserve boundaries rarely coincide with natural species distributions but are largely politically determined (Schonewald-Cox and Bayless, in prep.). It is therefore not surprising that boundaries, invasions and adjacent land uses are likely to present novel selection pressures (Liu and Godt 1983), with which genotypes of endemic species are frequently unequipped to cope.

The increasing modifications of natural gene exchange have powerful applications for conservation: for planning the preventive medicine of conservation, for diagnosing predispositions toward population decline, for detecting pending extinctions, and for administering measures intended to restore populations to "evolutionary" health (Schonewald-Cox et al. 1983). This paper focuses on the small population and explores practical techniques for maintaining the evolutionary health of populations and reversing declines in Hawaiian endemic populations.

WHY DO POPULATIONS BECOME SMALL?

Populations become small as a result of many environmental and selection variables (Beardmore 1983; Nei 1975). Catastrophic impacts, such as volcanic explosions, prolonged changes in climate, or new biological invasions, have probably accounted for the vast majority of declines and extinctions in past geological time. However, direct habitat elimination and exploitation, predation, disease, parasitism, and competition by newly introduced species have accounted for the loss of at least 60% of Hawaiian endemic bird species alone and undetermined numbers of other animal and plant endemics in the very constricted time period of 5,000 years (Olson and James 1982a and 1982b; James and Olson 1983; Atkinson 1977). Thus, populations can become small for a variety of reasons, and the rapidity with which extinctions are now occurring suggests that they are more cause- than time-dependent.

SMALLNESS AND SURVIVAL

From the standpoint of evolutionary genetics, species with genetically impoverished populations and species which have a narrow range of environmental tolerance are the most susceptible to extinction (Carson 1983; Beardmore 1983; Soule 1983). Smallness of populations is in itself a threat to many species, especially those that require large gene pools and depend

upon large amounts of gene flow for survival (Ralls, Brugger, and Ballou 1979; and Wright 1977 give examples for mammals). These species suffer from inbreeding depression and loss of genetic diversity when their populations become small. (Conversely, when gene flow is too rapid or barriers between previously distant populations are broken down, the swamping effect can be equally damaging, resulting in an outbreeding depression or heterosis.)

Species that typically inbreed or self-fertilize are likely to survive if they are flexible. Flexibility is limited by the amount of genetic diversity (alternate alleles and complex inter-gene relationships) carried by the genotype (Liu and Godt 1983; Clegg and Brown 1983). Nei, Maruyama, and Chakraborty (1975) demonstrated that a population must be quite small to lose substantial allelic diversity. Alternatively, if the population lacks diverse genotypes, then species survival requires the availability of other populations for recolonization (Selander 1983).

WHAT IS A SMALL POPULATION?

A population can be considered small with one or a thousand individuals, depending upon characteristics of the species. A "small" population is extinction-prone because it is demographically unstable or possesses too little genetic diversity to retain its evolutionary potential (e.g., ability to adapt and potentially give rise to other species). A population which retains about 90% of its genetic diversity is said to be at or above the genetic estimate of minimum effective population size and is said to retain its long-term evolutionary potential. On the other hand, a small population (below the minimum effective population size) retains too little diversity and is prone to too many genetic problems to maintain its evolutionary potential (e.g. ability to adapt and potentially give rise to other species).

Effective Population Size

The "effective population size," usually referred to as N_e, is the theoretician's parallel to the actual population size and is based in part on the number of males and females contributing to offspring in any one generation. Several baseline assumptions are made in determining the effective population size. In the case of small populations, N_e is the size an ideal population would have to be in order to experience the same rate of drift and decrease in variability as the study population. For example: In a study population of 50 individuals, there may be only 2 males and 10 females that mate to produce 1 offspring per female in the following year. A crude estimate of the effective

population size would be about 12. The effective population size is derived and described in varying levels of detail in evolutionary and population biology references. (See Wright 1978 and Crow and Kimura 1970 for derivations and theory; and see Frankel and Soule 1981, Soule and Wilcox 1980, and Schonewald-Cox et al. 1983 for use in the conservation context.)

Minimum Viable Population

The objective in conservation is to maintain populations at--or restore them to--levels matching the minimum requirements for survival. There are no fixed formulae for determining the exact minimum requirements for population size. However, some useful attempts have been made to generate estimates. The first estimate was generated by Franklin (1980) based on his analysis of _Drosophila_. The figure of 500 suggested by Franklin is currently being reexamined in light of new developments in conservation biology, genetics, and demography. Soule (pers. comm.) and a number of geneticists and demographers have collaborated to produce a new interpretation of minimum population requirements. Based on homeothermic vertebrate biology, they suggest that a few hundred animals (effective size) are necessary for minimum demographic survival. This number would just maintain population growth despite consistent mortality rates (due to individual cause of death or across-population causes of death). If periodic catastrophic events are included, the "few" hundred required in a stable environment may already be a small number relative to the need for survival.

THE EVOLUTIONARY POTENTIAL OF SMALL POPULATIONS

How genetic diversity is distributed within a population depends upon the mating system and upon environmental selection. Genetic diversity is manifested in several ways. _Between_ populations it is manifested in different allele frequencies, different alleles, and different multi-gene relationships (including polygenes and overdominant genes). _Within_ populations it is manifested in polymorphism, heterozygosity, polygenes, overdominant genes, and polyploidy.

In nature, several opportunities exist for increasing genetic diversity in populations. Beardmore (1983) summarized 4 basic sources of population diversity:
1. Recurrent mutational changes.
2. Inflow of genes from other populations, or species "migration".
3. Stochastic processes such as genetic drift.
4. Some form of selection that favors population diversity.

When populations become small and are isolated, the potential for new genetic variation to enter the gene pool becomes reduced; in addition, genetic diversity within the population is eroded. A small population of a cross-fertilizing species represents only a fraction of the diversity of its original population (sampling effect).

Typically Out-Breeding Diploid Species

For typically out-breeding species, 2 principal interacting factors can precipitate extinction. First, there is genetic drift which occurs even before the population becomes small. Genetic drift is the random loss of alleles and change in allele frequencies that result from sampling with each sexual reproduction. Alleles that occur in non-reproducing individuals decrease in frequency in the population, and if they are rare alleles and occur exclusively in individuals which have not reproduced, they are then lost altogether from the population unless they are restored by immigrants from another population (gene flow).

Secondly, there is the sampling effect of the population reduction itself. In a small population, more is lost than rare alleles. The otherwise normal genetic drift is exaggerated synergistically by the loss of some rare and potentially common alleles because fewer individuals remain to reproduce. These remaining individuals represent only a fraction of the allelic diversity of the original population. Thus, there is not only a change in allele frequencies, but an outright loss of alleles as well. Futuyma (1983) suggested that this extreme sampling generally results in a decrease in frequency of beneficial alleles and a concurrent increase for deleterious ones.

As population size decreases, allele diversity declines more and more due to the sampling effects of genetic drift and population reduction mentioned above. This is manifested in narrower mate selection which increases the likelihood of mating between individuals related by descent. Inbreeding, when it occurs in a species that is not adapted to this sort of mating strategy, can overtake the initial cause of population declines and drive populations to extinction. When related individuals mate, deleterious recessive alleles that are normally hidden in heterozygous recessive condition are expressed homozygously. The array of deleterious, recessive alleles is called genetic load. Genetic load occurs in the genome at a rate that is relatively constant for each species. It is speculated that 1-1.5% of alleles in humans are deleterious, but genetic loads for most species are unknown. Inbreeding also disrupts the balance of polygenes (Carson 1983),

and it can interfere with or eliminate overdominant
genes (Futuyma 1983).

When outbreeding species are forced into inbreed-
ing, "inbreeding depression" results from the inter-
action of the following: the expression of deleterious
recessive alleles caused by inbreeding; the loss of
alleles caused by the sampling effect of small popula-
tion size; and the increasingly reduced representation
of alternate alleles in the population. The combined
effects of these are lower survival rates and eventual
population decline.

To summarize, the most serious consequences of
small population size for species that store genetic
diversity within the population are loss of alleles and
inbreeding depression and population decline.

Polyploid and Typically Inbreeding and Self-Fertilizing Species

In polyploid species, which are typically inbreed-
ing and self-fertilizing, inbreeding and loss of al-
lelic diversity within the population do not pose the
same threats to survival as they do to diploid, out-
breeding species. However, even in its ultimate form
of self-fertilization, inbreeding leads to a uniformity
in the population which makes the population especially
vulnerable to climatic or other environmental changes.
Loss of variability may not become serious in the ab-
sence of habitat change or when selection is relaxed.
However, environmental, social or ecological stresses
may require characteristics that genetically depauper-
ate populations have lost. One of the most serious
consequences of small population size for species that
store genetic diversity between populations is the loss
of genetic sources (other populations for recoloniza-
tion), should local extinction occur.

DIFFERENCE BETWEEN SMALL POPULATIONS NOW AND AT INITIAL COLONIZATION

Species that first colonized the Islands experi-
enced stresses likely related to levels of inbreeding,
as well as changed food or climate regime and geologi-
cal stresses; but competition stress was probably not a
factor. Progressive colonization by diverse species
together with their expansions and divergences eventu-
ally led to competition stress.

Disequilibrium -- Adaptation

Environmental stresses peculiar to the Hawaiian
Island chain probably changed over tens or hundreds of
thousands of years. Species had to continuously adapt
to these changes in order to survive into the paleo-
archaeological period. This period changed the rate of

mortality of individuals and consequently of species. Selection pressures for adaptation to direct and indirect human modification of habitat intensified, only to reach cataclysmic proportions in the last few hundred years. Mutation rates are not known to accelerate in response to habitat deterioration, intense predation, depredation or competition. Changes by either mutation or recombination occur in response to generation time and population growth rates.

Threatened and endangered endemics have experienced negative population growth rates. Therefore the opportunity for adaptation has, if anything, decreased while the demand for adaptation has accelerated. For example, the extreme changes of stream temperatures to as much as 10 to 11 C above normal (in daily fluctuaaion as well as the absolute temperature, J.D. Parrish, pers. comm.) exclude native Hawaiian freshwater fishes and favor alien species competitors. The latter, being tolerant of temperature fluctuations, are now replacing endemics in reconstructed cement-lined stream channels, adding competition to the temperature stress of endemics.

Disequilibrium -- Species Turnover
Selection processes (now influenced by man) do not recognize value differences between endemic and alien species that man does. By attributing value to some species that can no longer survive on their own and eliminating others that would normally replace the declining ones, man decreases the ease with which some ecosystems can sustain themselves, and increases the difficulty we will face in trying to maintain evolutionary dynamics of native species in the Islands. Selection pressures have changed in category and intensity over the past several hundred years as a result of natural events and man's influences. Selection is now demanding adaptational changes on the part of endemics which they may never have had the capability of meeting, since their previous successes were based on entirely different packages of tolerances and pressures.

ASSESSING AND IMPROVING
A SMALL POPULATION'S CONDITION

Fortunately for the conservation community, the agricultural and sporting industries have had an age-old interest in manipulating small populations (cattle, Bos taurus; goats, Capra hircus; horses, Equus caballus; pigs, Sus scrofa; cats, Felis catus; dogs, Canis domesticus; decorative plants, etc.). While the techniques they employed were not, and frequently still are not, developed from population or evolutionary genetic theory, the practical experience and techniques derived from trial and error have contributed a great deal of

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guidance on the preventive and remedial measures useful for dealing with captive populations. The cattle industry, for example, has used the practice of maintaining stud books and pedigrees which recently has been combined with newly acquired knowledge of genetics to develop inbred lines of cattle that are now free of any lethal characteristics (Lasley 1978). Borrowing from this technology, some of the major zoological parks have begun to record pedigrees in order to determine levels of inbreeding (see Ballou 1983) and thereby influence reproductive success (Foose 1983; Ralls, Brugger, and Ballou 1979; Ralls and Ballou 1983).

There is a 180-degree difference in the evolutionary implications of management objectives of the cattle breeder and those of the manager of species for conservation. Typically, commercial interests impose heavy selection and controlled mating in order to narrow the characteristics expressed by a line to a specific set of desired qualities. Those qualities must occur with predictable intensity every time members of the line are mated. Inbred lines that are free of lethal alleles are especially prized. The breeder also hopes that the line will exist in "perpetuity" (in commercial terms, the lifetime of the breeder's economic motive or company). Because the environment in which the animal or plant lives can be controlled almost entirely, the breeder may feel that there is no need to maintain within-individual variability--at least it does not seem so for the evolutionary short term--but lack of genetic alternatives make the industry particularly vulnerable. If, with wheat for example, a new disease appears to which none of the domesticated strains have any resistance, the distance between mass human starvation and sufficient wheat may be measured by the availability of alternate and variable genotypes.

Populations ex situ

The optimum objective of zoological park conservation programs is to maintain populations for eventual restoration to the wild. Zoological park breeding programs follow 2 management approaches to accomplish this objective.

The first approach consists of obtaining animals from the wild which are then bred and periodically exchanged with other institutions. This provides gene flow between captive populations. These captive or semi-captive populations serve to stock other zoological parks and furnish the eventual founders for restoration programs. Frequently, though not always, numerous sources exist for gene flow so that considerable genetic diversity is stored in the whole of the international captive network (see Flesness, Grahm, and

Hastings 1982; and for International Species Inventory program (ISIS), see Foose 1983; Benirschke 1983).

In the second management approach, inbreeding is used deliberately when only a very few individuals exist in captivity and none are available from the wild to provide gene flow. In this case, inbreeding is totally unavoidable if the species is to continue. This approach is also used when a population is to be kept small and isolated, e.g. for exhibits, with no intention to restore members to native habitats. In this approach, mate selection is manipulated to adapt the population to inbreeding while simultaneously minimizing inbreeding depression.

In both management approaches, unlike those in commerce, the objective is to minimize selection (with the exception of selection for inbreeding tolerance in the second approach) and to avoid loss or skewing of allele frequencies. This is a very difficult task. Inadvertent selection introduced by diet, pen conditions, and veterinary care may increase selection pressures not favorable to eventual restoration of the species to the wild. Alternatively, management may unintentionally reduce selection for alleles of special value to survival in the wild. The strategy that managers of zoo populations take to minimize unnecessary impositions of selection is to spread mating among the largest number of individuals or to increase gene flow when possible by including individuals from wild populations.

Under captive conditions, it is possible to record which animals are being mated and to maintain a pedigree that is checked every time a choice of mates is to be made. This reduces accidental matings between individuals related by descent and significantly improves survival for captive populations. Ballou (1983) demonstrated in detail how the pedigree can be used to calculate the inbreeding coefficient. The inbreeding coefficient is a valuable tool for determining whether, and to what extent, individuals are inbred.

Populations in situ
Unfortunately, in conditions such as those that exist surrounding semi-wild or free-roaming populations, mating cannot usually be controlled nor can pedigrees be easily maintained, even if mating behavior is monitored. For example, with some carnivores, ungulates or primates, and many other groups, attempted fertilizations can involve more than one male, and it cannot be determined exclusively from field observations which male is actually responsible for fertilization. Hence, it is difficult to establish population health genetically.

Laboratory techniques, such as isozyme electro-
phoresis and karyotyping, can estimate the amount of
variability in populations (Benirschke, Lasley, and
Ryder 1980; Allendorf 1983; Hamrick 1983; Chambers and
Bayless 1983) or can detect abnormal chromosome numbers
or gross mutations in the chromosomes. However, these
techniques provide no useful information for estimating
levels of inbreeding in non-captive populations. A
search for alternate means of determining inbreeding
coefficients when no pedigree is available has revealed
that mitochondrial DNA (mtDNA) analysis may have the
greatest promise. (See Powell 1983 for a discussion
and example of mtDNA analysis for the mosquito Aedes
aegypti.)

Because of its potential benefit to conservation
of species in natural habitats, the method and use of
mtDNA analysis deserves some description. Fortunately,
the technique has gone beyond use with Drosophila and
is presently being applied to vertebrate populations,
e.g. lizards (A.R. Templeton, pers. comm.). Analysis
of mtDNA involves the electrophoresis for DNA segments
that are cut by restriction endonucleases at specific
recognition sites. The DNA of the mitochondrion is
single stranded and circular (reminiscent of bacterial
DNA) and can be mapped, cut and accounted for far more
easily than the vastly larger and more complex system
of nuclear chromosomes. Because mitochondria are gen-
erally inherited with the egg, they can act as tracers
for female lineages with a small margin of error. The
experiments presently being conducted use pedigree data
and anatomical markers to test the reliability of the
assumptions of heritability and uniqueness of markers
for each individual. The mtDNA technique has the po-
tential of circumventing the use of pedigrees for de-
tecting inbreeding levels. Depending upon species
chromosomal arrangements and sexual dimorphism of
chromososmes and gametes, additional markers can be
applied to males (as on the Y chromosome).

So far, researchers are using both female (mtDNA)
and male (sexual or autosomal) markers. It may not be
easy to identify male markers for many species stressed
in conservation programs, and until male markers are
identified, it is desirable that we find an interim
method, even if it is less exact. One such method
would combine the results of mitochondrial analysis
with known data on relevant population and behavioral
parameters for inference of an approximated inbreeding
coefficient. This approximated coefficient then could
be used similarly to properly document inbreeding coef-
ficients for planning population management. It is
hoped that, based on controlled laboratory experiments,

a predictable margin of error for the inference could be established.

CONDITION OF HAWAIIAN ENDEMICS

The entire native fauna and flora in the Hawaiian Islands was established from small groups of founders or single colonizers that, for the most part, never received subsequent gene flow from any mainland or other island.

Surviving Colonization

In order for a species to survive colonization with only one or a few founders, it must be able to withstand the deleterious effects of inbreeding and the other stresses of small populations (Carson 1983). This can occur in several ways, including combinations of the following, if:

1. The founder is self-fertilizing.
2. The founder is an immigrant from an already inbred population.
3. The founder carries few deleterious alleles, or the deleterious alleles carried are not lethal in the new environment even though they may have decreased overall fitness.
4. The founder successfully reproduces, competes for, and expands its range in the habitat, and competes successfully to maintain the niche.
5. The founder experiences selective release with abundant food source and no (or little) predation.
6. The founder finds an abundance of resources and open niche space.
7. One or more additional founding events by the same species occur soon after the initial one, though it may not necessarily be from the same source.

Historical Influences on Survival

It may be that during their initial colonization period, Hawaiian endemics experienced a strong, internally directed selection to overcome small population size and inbreeding depression. As the numbers of species increased on the Islands, such factors as predation and competition, combined with environmental fluctuations, may have kept populations small or subjected them to repeated bottlenecks. Many Hawaiian endemics may have been already adapted to inbreeding and small population size early in their island histories. Regardless, with the arrival of humans on the Islands, reduction in population sizes caused by hunting, coupled with severe environmental selection caused by invasions of alien organisms, habitat elimination, and relegation of populations to marginal habitats, necessarily intensified selection for tolerance of small population size and inbreeding tolerance.

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The work of Olson and James (1982a, b; James and Olson 1983) suggested that the first major extinctions of Hawaiian endemic bird species began about 1,500 years ago. The agents of destruction were human: deforestation carried out for the benefit of agricultural development, introduction of the rat (Rattus exulans) and pig (accompanists of the Polynesians; Atkinson 1977), and hunting of flightless species for food. In 1982, the published results of Olson and James (1982a, 1982b) pointed to the extinction of approximately one-half of the Hawaiian endemic bird species while Polynesians occupied the Islands; only about one-third of the original diversity remains after the appearance and settlement by contemporary cultures in the Hawaiian Islands. Most radical in their declines were the non-passerine species, including geese, owls, and crows, of which only 15% or fewer remain.

Modern Prospects for Survival

Species plummeting to small population sizes and faced with inbreeding and allele loss are re-experiencing colonization, this time on habitat islands within the Hawaiian Islands. As probably occurred historically with the new arrivals, some species will adjust and survive and some will fail. It will not be possible for all the threatened species to retain and recolonize the identical niches they once occupied. Both species populations and niches have changed permanently in many cases.

Species that are island endemics have no possibilities for range expansion or for the reception of gene flow from sources other than in the Islands. With much of the natural lowland habitat converted to private use, it is reasonable to expect that restorations to levels above minimum effective population sizes for many endemic species near extinction are no longer possible; nor can we foresee that some populations will ever grow beyond the small, and possibly inbred, level in the near future.

This island scenario has its closest parallel (though it is a weak one) in zoo populations of species which are functionally extinct in the wild, and whose populations in captivity are the only hope of preserving the species.

INBREEDING AND HAWAIIAN ENDEMIC DIPLOID SPECIES

In small populations, inbreeding is affected by the sex ratio, mating system, mating system flexibility (or options of several mating systems available to a species), overlap of generations, the number of times the individuals mate, the production of single or many young, and the generation time. Allele loss is

aggravated by slow population growth. Inbreeding is aggravated if the sex ratio is unequal (as with polygynous species), and becomes a function of the number of females and males, independently:

$$\frac{1}{N_e} = \frac{1}{4N_m} + \frac{1}{4N_f} \quad \text{or} \quad N_e = \frac{4N_m N_f}{N_m + N_f}$$

(where N_e is the effective population size, N_m is the number of males and N_f is the number of females) (Frankel and Soule 1981). However, it seems that by far the majority of endangered endemic bird species in the Hawaiian Islands is predisposed to monogamy (Shallenberger 1981), and this type of mating system tends to equalize genetic contributions by individuals. Equalizing contributions to subsequent generations will tend to reduce the rate at which heterozygosity is lost and at which the genetic load is exposed. For species that are not potentially inbred or that still exist in large numbers, monitoring for sudden declines and inbreeding is most essential.

In a study of a polygynous species, North American elk (Cervus elaphus), Schonewald-Cox, Baker, and Bayless (in prep.) conducted an analysis of founding events that were part of restoration programs. They found that conventional restorations tended to use from 4 to 25 individuals with little regard for demographic composition. They hypothesized that the first year's increase in level of inbreeding ranged from 22% to 3.6% (for 4 to 25 individuals respectively) which 20 years later, for example, would cause the populations to have inbreeding coefficients ranging from 1 to 0.41. The safe increase in the inbreeding coefficient given by Lasely (1978) for domestic cattle for one generation is 0.01. For comparison, the inbreeding coefficient of an individual produced by a brother-sister mating in a normal family is 0.25 and for first cousins is 0.06. With time and in the absence of gene flow, the percent relation only increases. While the increases in inbreeding coefficients for monogamous species do not occur as quickly as with polygynous species of the same size, the tendency for inbreeding with small population size for any mating system is still quite high. Species that have gone through bottlenecks have been affected by small population size and inbreeding, and it may very well be that the series of bottlenecks experienced by some declining Hawaiian species may in fact have already converted them to strongly inbred lines. The fact that some of these persist suggests that they may have adapted to inbreeding, at least for the short term.

RESTORING SMALL POPULATION REMNANTS
OF DIPLOID SPECIES WITH INBREEDING: A CASE EXAMPLE

To reverse population decline and inbreeding for Speke's gazelle (Gazella spekei), Templeton and Read (Templeton 1980; Templeton and Read 1983) applied Templeton's findings on the adaptation of Drosophila populations to inbreeding. The Speke's gazelle, numbering 25 when Templeton and Read began the project, originally consisted of 4 founders, 1 male and 3 females. Calculating the effective population size of the founder herd, and incorporating the effects of highly differential contributions by the founders to the progeny, they obtained N_e = 2 (where N_e is the effective population size). The population was both inbred and suffering from depression. Taking into account that no other source existed for gene flow and that this species was nearly extinct in the wild, Templeton and Read decided to tackle the problem of inbreeding depression by using a controlled application of inbreeding. The decision to use this approach may be especially pertinent to the current situations existing for endangered Hawaiian species and therefore is described in some detail.

Adapting to One's Genome
First, Templeton and Read (1983) justified adapting a normally outbreeding species to inbreeding by using the hypothesis that individuals in a population are not only adapting to their external environment but to their internal genetic environment as well. Adaptation to genetic load is greatly influenced by the mating system of the species population. Templeton and Read (1983) pointed out that the symptoms of inbreeding depression (changes in fertility, birth weights, survival) are reminescent of the symptoms that result from failure of a species to adjust to rapid environmental changes. Although deaths from inbreeding depression are almost never traceable to a single allele, the death which typically occurs early in life can be said to result from one to several deleterious alleles formerly carried recessively in the genome (see Ralls, Brugger, and Ballou 1979).

Adapting to Inbreeding
Templeton (1980) showed that adaptation to inbreeding can be achieved regardless of population size. That this can be achieved rapidly and successfully is a major breakthrough in the application of genetics to conservation of small populations of non-typically inbreeding species. He suggested that this is done most successfully and rapidly when "genetic variability is maximized" at both the individual and population level. The following summary is a series of "rules" for selecting mates and for achieving the

adaptation to inbreeding that is recommended and elaborated upon in Templeton and Read (1983):

First and foremost, the objective is to increase population size as rapidly as possible before and during the implementation of the breeding program.

Secondly, as concerns the selection of characteristics for the mates:
1. Parents, in combination, must maximize genetic variation.
2. Parents must be healthy.

Thirdly, as concerns the selection of characteristics that the offspring will receive from the parents:
1. Offspring should have maximum genetic variability in terms of founder ancestry.
2. Offspring should be the result of inbreeding, but not extreme inbreeding.

In order to accomplish the basic genetic planning for this work, one needs only the pedigree data for the population. Therefore, for any critically endangered population that is maintained in semi-captive or captive conditions, it is essential (to the extent feasible) to maintain pedigree data. (In most cases, where we deal with wild populations, pedigree data are not necessarily available; then the mtDNA techniques discussed in the last section become increasingly useful.)

Increasing the population size rapidly is mandated in order to decrease the probability of extinction and to help reduce the potential for loss of rare alleles remaining in the population. It also helps during a transitional phase from outbreeding to inbreeding to increase the number of combinations of individuals that can be mated, a situation that will reduce the abruptness of the change warned against as "extreme inbreeding." Further, the rapid increase in population size also reduces the number of generations that will be vulnerable to inbreeding depression (see also Templeton 1980; Foose 1980; Frankel and Soule 1981). To accomplish this desired end, some innovative techniques have been used with success. Among these have been egg or embryo removal from a female of the targeted population and implantation into a surrogate mother of a foster species. How quickly the transition phase passes from outbreeding-adapted to inbreeding-adapted is dependent upon the amount of genetic variability remaining in the population (including that remaining in the individuals).

Healthy and inbred parents predispose their offspring to be healthy also. Therefore, individuals which are inbred but do not show any obvious

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deleterious manifestations of inbreeding are optimal choices for mates. The availability of such animals makes the transition faster and more efficient.

In their next step, Templeton and Read calculated the percentage contribution of each of the original founders to the present gene pool. They found that ideally, with 4 founders, each should have contributed 25% of the matings to the present-day gene pool. Such equalized contributions guard against loss of alleles, maintain heterozygosity, and therefore reduce exposure of genetic load and disruption of polygenes and over-dominance relationships between alleles. The authors calculated the inbreeding coefficient for each poten-tial parent to select for high coefficient and good health. However, they did not recommend taking indivi-duals with the most extreme inbreeding coefficients and mating these to each other first in order to speed the transition, as they may cause too abrupt a change, thereby increasing the probability of extinction.

In order to maximize the genetic variability of the offspring, Templeton and Read suggested selecting parents which, when mated, will produce the most even overall representation of the original founders (equiv-alent contributions of genome by percentage). Such re-sults are accomplished most easily by picking parents with different ancestry (called disassortative mating with respect to pedigree). As Averhoff and Richardson (1976) and Templeton (1980) suggested, disassortative mating reduces the loss of alleles and maintains het-erozygosity. It also prevents the acceleration of inbreeding at a harmful rate (see also Falconer 1981) that could cause both loss of alleles and negation of the adaptation (attempt) to inbreeding, as well as "transilience" (a condition in which rapid changes in traits may occur, producing undesired results). Thus, ideal mates that maximize genetic variability in the offspring are those that cause the offspring to bear alleles from all of the founders (stored in heterozy-gous condition resulting from the combination of ga-metes, and determined through the random assortment of alleles during meiosis when gametes are formed).

The last objective (but not the least in impor-tance) is to slowly increase the inbreeding coefficient of the offspring. Thus, combinations resulting in non-inbred offspring as well as extremes of inbred off-spring are avoided.

Two Notes on the Method
It is important to note that just because an in-dividual carries deleterious alleles does not automati-cally mean that the entire genome is inferior. On the contrary, the individual may be carrying rare alleles

that could be lost if it is excluded from the gene pool. By equalizing founder contributions, Templeton and Read (1983) alleviated this problem. However, there is no guarantee that this loss of rare alleles will not potentially occur. Adaptation to inbreeding is a treatment of last resort and addresses only the short-term hurdle of inbreeding depression.

In the "wild" the greater hurdle of adapting to rapid environmental changes cannot be solved with adaptation to inbreeding, alone. This is one of the lessons that the slugs Arion and Limax offer (Selander 1983). Long-term survival, in the face of today's intensity of selection pressures, requires something that maintains rare alleles and encourages the development of novel and beneficial alleles, a process that generally requires both luck and thousands if not millions of generations in nature.

SMALL POPULATIONS OF SELF-FERTILIZING
AND POLYPLOID SPECIES

Selfing and (even number) polyploid species have a slightly easier task in adapting to colonizing situations (Selander 1983; Hamrick 1983; Clegg and Brown 1983), because the problem of mate selection and reproduction is reduced, even if population density and population size are very low (Selander 1983; Stebbins 1957; Baker 1959; Ghiselin 1969). A succession of bottlenecks after initial colonization (perhaps by a single individual) predisposes selection for the alleles determining self-fertilization. Species which typically inbreed (especially self-fertilizing species) do not experience the same level of "hybrid" vigor as outbreeding species that, having been inbred, are subsequently mated betwen lines. The fact that a population or species is adapted to self-fertilization or inbreeding suggests that advantages exist for populations that colonize readily with few individuals, sustain bottlenecks, are locally uniform, and store genetic variability between populations that may occasionally meet. Concurrent disadvantages also exist in that, while highly homozygous individuals or homozygous populations are very plastic, they are not easily adapted to sudden environmental or other selection changes and thus are extinction prone (Selander 1983). In other words, homogeneity of these species in new environments may favor survival and colonization, but when the environment changes suddenly, homogeneous colonizers are less able to adapt and may fail to survive.

One might suspect that highly inbred or selfing populations may not suffer from the repeated bottlenecks and habitat elimination in climatically stable areas such as the Hawaiian Islands. However, the

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drastic reduction of forest by humans, and the intro-
duction of new diseases, parasites, predators, and
depredators certainly have constituted severe environ-
mental changes.

Restoration for self-fertilizing or polyploid spe-
cies may be somewhat easier, however, than for diploid
species. For plants, efforts with vegetational propa-
gation, self-fertilization, and separation of indivi-
duals to found new lines, mimic an already successful
agricultural and horticultural strategy. Highly inbred
or selfing species usually have close relatives or
other populations with which they are reproductively
compatible (say, in captivity) or from which they were
recently separated; for some, the gross morphological
differences among subspecies, varieties or lines are in
part a manifestation of phenotypic adjustments combined
with sampling efforts derived from colonizations and
subsequent bottlenecks. An option exists to ensure
against the extinction proneness of syngenic lines,
that is, to cross some lines to form new gene combina-
tions that might withstand the new stresses; this
risks, of course, the occurrence of heterosis (out-
breeding depression). In addition, for these spe-
cies, mixing of closely related varieties should not be
discouraged as a last resort strategy to promote survi-
val. Adapting species to manipulated changes in their
genomes will be the new management challenge in endan-
gered species restoration.

It is unfortunate that most of the applications of
genetics to polyploid and self-fertilizing species are
in agriculture, where selection is made narrow. In
conservation, however, we hardly know what we should
select. The formation of numerous lines and small
populations throughout available habitat will allow na-
ture to make its final choices in the face of change.

A THOUGHT ON ESSENTIALLY EXTINCT SPECIES

Schonewald-Cox, Baker, and Nakamura (in prep.)
have proposed a means of closing the gap between in-
breeding depression in small populations and adaptation
demands addressed earlier for new and especially in-
tense environmental stresses caused by human habitat
modification. They assert that the techniques applied
to the dusky sea-side sparrow (Ammospiza nigrescens)
can be refined and adapted for island use with endemic
species that are on the brink of extinction, specifi-
cally species that have close (genetically compatible)
and traceable ancestors existing elsewhere. This, they
assert, can be accomplished without necessarily inter-
fering with the survival of the vanishing population
remnant. The vanishing remnant could be treated simul-
taneously as Templeton and Read (1983) suggested. In a

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manner similar to what was done for the dusky sea-side
sparrow (H. Kale, pers. comm.), semen is taken from one
to several males of the endemic. The semen is used to
inseminate females from various localities of the an-
cestral habitat, particularly areas where the ancestral
species is successful in the face of modern human-
related stresses. Efforts are made to not inseminate
offspring with the same individual's semen that was
used for the mother. The first generation offspring
are (roughly) half of each, ancestor and endemic. In
the next generation, the female offspring are 0.75
endemic and 0.25 ancestral. By the fourth generation,
the offspring are 93.7% endemic and by the tenth gener-
ation they are 99.9% endemic. This is based on a sim-
ple and generalized manipulation:

$$\% \text{ endemic genome} = \frac{[(2^t) - 1]}{2^t} \times 100$$

(in which t is the number of the backcross in the se-
quence). Note that the process becomes more complex if
additional females are brought from new sources into
the captive population. If females are selected from
numerous habitats, different lineages can be tested for
their environmental tolerances. This could help pre-
determine which individuals and their descendants might
be potentially successful in different parts of the
former range of the endemic species (in which the en-
demic can no longer survive). The developed (99.9% or
more) endemic population(s) can be held until the natu-
ral population dies out and then used as a new founder,
or it can be used to colonize other parts of the endem-
ic's former range where natural selection can then
determine whether this endemic with introduced (in-
fused) alleles has a chance or not.

Once refined, such an approach could help bring
back not only the vestiges of dwindling species, but it
may offer nearly extinct species a chance to use modi-
fied niches with new vitality. Heterosis and other
dangers of mixing 2 forms are risked, but this is done
ex situ and under controlled conditions. This is a
more realistic approach than trying to adapt a dying
species to the principal selection pressures of the
past, or preserving (as opposed to conserving) a spe-
cies adapted to selection pressures driving the species
to extinction in the present. Needless to say, this is
not the ultimate answer, but a step that has a poten-
tial to work some of the time for some of the species.

CONCLUSIONS: GENETICS, MINIMUM POPULATION SIZE, AND THE PROSPECT FOR HAWAIIAN SPECIES

The conservation problem of Hawai'i, fortunately, is one for which a great deal of specialized expertise is already available and interested. It may turn out that some aspect of genetic management for a few species may be one of several contemporaneous solutions. However, the conflict between species loss in the Hawaiian Islands, the highly specialized and complex niche relationships that Hawaiian endemics have developed, and economic development for an ensured profit may be irreconcilable.

Franklin (this volume) and also Frankel(1984), di Castri and Hadley (1984), and di Castri, Baker, and Hadley (1984) have spoken to the need for making additional habitat available, as have many others dealing with tropical and island extinctions. The Hawaiian Islands are the worst of all possible worlds in that many of the remaining passerines and plants not already extirpated by Polynesian deforestation are now endangered by current, continuing deforestation and other perturbations. The second wave of alien organisms that arrived with contemporary cultures only hastens the process. The theoretically obvious option of manipulating populations that remain, to adapt them to more generalized habits or marginal habitats, as well as to continued inbreeding, may prove inadequate for saving most of the remaining endemics. To restate what was said at the beginning of this paper, catastrophic changes are too rapid presently to allow species to naturally adapt. They even have trouble increasing in numbers, a baseline requirement for overcoming both external pressures and those derived from their own genomes. Certainly, for species that are still found in moderate numbers, as well as for species that are very close to extinction but with potential for recovery, the following steps should be considered.

First, determine whether the population is already isolated and adapted to inbreeding. If this is not known, survey the population's movements, including dispersal. Note the sources and destinations of dispersers, and measure their reproductive success. Isolation needs to be determined on both a short (single survey) and longer term (several years) level to determine whether apparent isolation or movement is, in fact, resulting in gene flow or inbreeding and isolation. It is important to determine even slight levels of gene flow. Even with high levels of inbreeding (see Wright 1978 and Chesser 1983), a very small amount of gene flow can be enough to prevent loss of rare alleles (an optimistic note).

Second, if the focal population is already adapted to inbreeding, then separate and isolate a number of small founder populations (as is feasible) throughout pockets of available habitat. Lines can be observed for their tolerance to marginal habitat conditions and placed accordingly. Namkoong (1983) had some suggestions on how this might be accomplished.

Third, if populations are not already adapted to inbreeding (i.e., their fecundity, survival, etc. are very low), then remove individuals and establish several small populations in captivity (for species that can survive in captivity). Inbred lines can be developed and subsequently released in isolated pockets to let nature take its course from there.

And, consider a fourth step of using controlled backcrossing to regenerate other populations in captivity or other habitats formerly occupied by the endemic species that have a potential to survive modern stresses.

ACKNOWLEDGEMENTS

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