Genetics and the Conservation of Animals in Fragmented Habitats

David S. Woodruff

ABSTRACT
Traditionally, threatened species conservation has involved ecological management as extinction is fundamentally a demographic event. In the future we will also have to consider genetic aspects of species endangerment as inbreeding and the loss of genetic variation erode the viability of small and fragmented populations. First, the management options to maximize the genetically effective size of a population ($N_e$) are outlined together with other practices designed to conserve innate genetic variation. Second, the increasing role of genetic data in the definition or characterization of evolutionary significant units for conservation management are illustrated; examples of the inadvertent mixing of genetically similar populations are discussed. Existing techniques for monitoring genetic variation and assessing genetic relationships are reviewed and new methods based on non-invasive DNA sampling and direct sequencing are described. Recently initiated studies of genetic and demographic effects of rainforest fragmentation on the viability of small mammal populations in Thailand are outlined. As habitat fragmentation, by outright deforestation and by forest degradation (albeit by selective logging), is proceeding at an alarming rate in Malaysia wildlife managers will soon have to cope with the genetic consequences of these practices.

INTRODUCTION
There are probably at least 10 million species of plants and animals on earth today and most of this biodiversity is confined to the humid tropics. Deforestation and forest degradation at rates in excess of 2% per year threaten half these species with extinction during the next century. This on-going extinction spasm, larger than anything experienced in the biosphere in the last 65 million years, will leave countries like Malaysia with an impoverished biota. Unique natural resources and the essential environmental services they provide will be lost forever. Although a few national parks and other protected areas are large enough to sustain wildlife naturally, most are not. Populations surviving on smaller habitat patches will inevitably require both demographic and genetic management if they are to avoid extinction. Saving biodiversity will ultimately require far more than simply reserving bits of habitat and letting Nature take her course. Far from being in harmony with nature, human societies have recently...
degraded ecosystems and perturbed the biosphere to the point that inter-
ventive management of nature is the only option left. The challenges facing
us are therefore to develop the techniques and the political resolve to apply
them in time to avoid what Edward O. Wilson has termed “the folly that
our descendants are least likely to forgive.” The 1980’s were marked by a
serious upsurge of interest in meeting these challenges and the 1990’s will
see the first major tests of the fruits of these scientific and political efforts.
In this paper I will focus on one rather narrow aspect of conservation —
namely the increasing need to manage genetic aspects of animal population
and species viability. My purpose is to show that although existing science
and technology are inadequate to the tasks facing wildlife and forest
managers, progress is being made. Appropriate methods and procedures
should become available in the next decade, in time for application to the
conservation of the surviving biota.

At the outset I must refer readers elsewhere, to other sources, for
comprehensive discussions of the importance of conserving biodiversity
and Woodruff (1989, 1991a and b). Similarly, useful background discussions
of the importance of genetics in the conservation of threatened species may
be found in publications by Frankel and Soule (1981), Schonewald-Cox
these references will provide the reader with a comprehensive overview of
the field of conservation biology. Simberloff (1988) provides a more detailed
review of the growth of this science and traces the historical roots of the
minimum viable population (MVP) concept and the related concept of
the metapopulation. Although we have passed the stage where the MVP
concept is of central concern, the latter concept has assumed increasing
importance. The metapopulation model has replaced the oversimplified
notion that a species can be considered as having a single geographically
all-encompassing population. Instead, we now recognize that species com-
prise groups of subpopulations with far less movement between such sub-
populations than occurs within them. Animal numbers may fluctuate in-
dependently within each subpopulation and small subpopulations go extinct
fairly frequently. Dispersal between habitat patches may subsequently
result in the recolonization of a patch. According to the metapopulation
model we therefore envision a species as comprising a large number of
small subpopulations linked by between habitat patch dispersal. Each
subpopulation has a finite probability of going extinct with the smallest
subpopulations “winking on and off” every few generations. This highly
dynamic metapopulation concept is the focus of much current research
and likely to form the basis of future management policies (Olivieri et al.,
1990).

CONSERVING POPULATION VIABILITY

The causes of extinction and extirpation are well-known and include
habitat loss and fragmentation, overkill, introduced species, secondary
cascade) effects associated with removal of keystone mutualists, and failure to evolve fast enough to biotic or physical changes in the environment. The ability of a population to adapt to the consequences of range fragmentation and other changes is determined, in part, by its innate genetic variability. Such variability is a characteristic of all living species and involves differences ranging from the single gene to the chromosomal levels of organization. Studies of allozymic variation in more than 1000 species first revealed the enormous genetic variability of natural populations; on average, 30% of all structural genes surveyed are polymorphic and individuals are heterozygous at 5-10% of such loci (Nevo et al., 1984). According to Fisher's Fundamental Theorem of Natural Selection it is this genetic variability that ultimately determines a population's ability to evolve, to remain evolutionarily viable.

As a generalization, genetic variation is a highly beneficial character and is positively correlated with such traits as growth rate, adult size, metabolic efficiency, fertility and disease resistance. The loss of genetic variation in a population therefore has serious harmful effects on that population's viability. Wildlife and forest managers will increasingly have to monitor and maintain the genetic variability of the populations in their care.

Genetic variation is thus an important component of population viability analysis (PVA) — a new methodology being developed to quantify overall persistence from a consideration of population genetics, demography, dispersion, dispersal and population structure. In PVA we recognize the important distinction between a population's actual size or census count \( N \) and its genetic effective size \( N_e \). The presence of non-reproducing individuals, unequal numbers of males and females, variance in family size, and the degree of inbreeding all reduce \( N_e \) to below \( N \). The effective size of a population can be 1 or 2 orders of magnitude less than the census size (Gilpin, 1987). For example, the Australian mainland population of eastern barred bandicoot, Perameles gunnii was found to have approximately 633 individuals but an effective size of only 67 (Sherwin and Murray, 1990). As \( N_e \) not \( N \) determines a population's fitness, evolutionary potential and extinction probability, many species with apparently adequate population sizes may actually be in genetic trouble already. The reader unfamiliar with this important concept is referred to Frankel and Soule (1981), Lande (1988) and Woodruff (1991a, b) for additional information.

The concept of the genetic effective size \( (N_e) \) allows us to estimate the genetic effects of range or habitat fragmentation. In the absence of factors promoting genetic variation (mutation and gene flow), uncommon variants are lost by random or chance events in a process called genetic drift. On theoretical grounds we know that the expected rate of loss of neutral variation may be very high in small populations of sexually reproducing species. The predicted rate of loss is \( 1/(2N_e) \) per generation and most of the variation in a small population can be lost in \( 2N_e \) generations. Thus a population with \( N=100 \) and \( N_e=10 \) can lose most of its variation in 20 generations. Habitat fragmentation reduces \( N \) rapidly and such demographic bottlenecks further reduce \( N_e \) by one or two orders of magnitude within a generation. Thus many fragmented populations of interest to wildlife and natural
resource managers are at high and immediate genetic risk.

The concept of \( N_e \) is also relevant to another serious threat to population viability, namely inbreeding. Inbreeding, or the mating of close relatives, may result in reduced viability and fecundity known as inbreeding depression. Inbreeding produces homozygosity of recessive deleterious mutants and, by chance, in small populations these alleles (contributors to genetic load) can become fixed. Again, when the number of genetically effective (unrelated) individuals is small, population viability is diminished.

As a rule of thumb based on centuries of experience with domestic animals, when \( N_e \) falls below 50 a population is predisposed to inbreeding depression. The problem is particularly noticeable when normally outbreeding individuals are forced to inbreed — as might occur when habitat is first fragmented and when new populations are founded with a small number of individuals. It is not surprising therefore that Ralls et al. (1988) were able to document inbreeding depression in many captive populations of mammals. Although all populations and species have the potential for exhibiting inbreeding depression, behavioral patterns have often evolved to avoid such problems. Similarly, populations with normally high levels of inbreeding are effectively purged of deleterious genes if the onset of inbreeding is gradual rather than sudden. Thus the black-footed ferret, Mustela nigripes, with very low \( N \) and \( N_e \) for at least 30 generations (Brussard and Gilpin, 1989) may not be at the same genetic risk as the African elephant Loxodonta africana, and black rhinoceros, Diceros bicornis, whose numbers have plummeted recently as a result of poaching and range fragmentation.

Earlier theoretical arguments held that to avoid the threat of inbreeding depression on short-term survival an \( N_e > 50 \) was required. Similar arguments were used to show that the long-term survival of a population required the amount of genetic variation typically found when \( N_e > 500 \). These generalizations and the derived 50/500 rule for managers are now seen as flawed and too simplistic. Debates concerning minimum viable population (MVP) size have rightly given way to population viability analyses (PVA) and the search for thresholds for sustainable population evolution. Similarly, the \( N_e \) concept, while still of central concern, is now recognized as being more complex. The interested reader is referred to Simberloff (1988) for a review of this complexity and a discussion of the differences between the inbreeding \( N_e \), the variance \( N_e \), and the random extinction or eigenvalue \( N_e \). Here it is sufficient to note that these various ways of considering the effective size of a population may or may not give the same result. In a growing population the variance \( N_e \) will typically be larger than the inbreeding \( N_e \); in a declining population, the reverse. Managers should therefore be differentially concerned with the effects of inbreeding and the loss of genetic variation depending on circumstances and objectives. While such generalizations have a strong conceptual base it must be remembered that estimating any \( N_e \) value is still very difficult in the field. The theoretical models and equations still lack operational utility and fail to deal adequately with either overlapping generations or metapopulations. Wildlife and forest managers should not be deterred by the inadequacies of existing \( N_e \) theory;
while awaiting the resolution of these largely academic issues they should continue to maximize $N_e$ whenever possible.

**TRANSLOCATION AS A GENETIC MANAGEMENT TOOL**

The variance $N_e$ can be increased locally by the judicious movement of individuals between subpopulations. Such artificial gene flow will counter genetic drift in effectively isolated subpopulations. The movement of very few individuals per generation is usually sufficient to overcome the effects or range fragmentation. It is best if the translocated individuals are moved between adjacent subpopulations rather than between distant parts of a metapopulation in order to preserve natural patterns of geographic variation. Only as a last resort should all a metapopulation’s genetic diversity be pooled to produce a homogeneous or generic population. Such management practices, with translocations replacing natural gene flow, have been suggested for the grizzly bear, *Ursus arctos*, population in Yellowstone National Park. This now isolated subpopulation numbers less than 200 individuals, has an $N_e$ of less than 30, and is exhibiting one symptom of genetic ill-health: declining litter size. To counter the effects of $N_e$ reduction associated with range fragmentation it has been suggested that one male bear be translocated into the park from adjacent Glacier National Park or the Canadian Rockies every 10 years (Lande and Barrowclough, 1987; Harris and Allendorf, 1989).

Countering the effects of range fragmentation by the judicious movement of individuals between subpopulations is not nearly as simple as it sounds. First, it typically involves cooperation between various branches of governments and the private sector (Salwasser et al., 1987). Second, it is not sufficient to simply move individuals — the translocated individuals must successfully mate and reproduce with the residents of their new habitat patch. The capture and transport of animals can have a high probability of causing death or injury. In the case of Sumatran rhinoceros, *Dicerorhinus sumatrensis*, failure at this stage is estimated to have a probability of 0.9 (Maguire et al., 1987). Even if translocation is successful, the introduced animals may die quickly in their new environment if they are unable to find food, water and shelter from predators. Exposure to new predators can be especially problematical. Success will also depend on the social competency of the translocated individuals in their new subpopulation (Strum and Southwick, 1986). Sex, social status, age, size, nutritional state and parasite load may all affect the future reproductive success of translocated individuals. There is also a danger that the translocated individuals will introduce a pathogen into the target population. Finally, philopatry may also create problems; every manager has tales of the remarkable journeys completed by translocated individuals that return to their original homes. It should not surprise us, therefore, that the science of successfully translocating individuals to stimulate natural gene flow between isolated subpopulations is in its infancy.

If translocating wild animals is challenging, the reintroduction of captive-reared individuals is even more difficult (Stanley Price, 1989).
Habituated animals are typically incompetent to fend for themselves and may require lengthy behavioral rehabilitation. Abandoned pets and zoo-born animals are poor candidates for return to nature without expensive preparation. For this reason, arguments that zoos can serve as effective sanctuaries for selected species until they can be safely reintroduced into nature a hundred years from now have major limitations. The reader is referred to Conway (1989) for an excellent review of current programs of short-term ex situ propagation and reintroduction. Unfortunately, successful examples involving Southeast Asian species are still practically non-existent although programs involving selected pheasants, Bali mynah, sarus crane and sea turtles are underway. In the present context ex situ care and biotechnology offer, at best, an expensive last resort when all hope of managing a species in nature is gone.

Managers may also employ judicious translocations to reduce the second genetic threat to fragmented populations: inbreeding depression in small isolated populations. Again, moving individuals between adjacent rather than geographically distant subpopulations is preferable as the latter may result in outbreeding depression. This latter phenomenon is observed when individuals adapted to or derived from different habitat patches hybridize. It can occur either because of local adaptation in a geographically widespread species and/or because of intrinsic coadaptation of genes and chromosomal complexes (Templeton et al., 1986). Outbreeding depression can disrupt locally coadapted gene complexes which, for example, confer disease resistance or the locally appropriate timing of reproduction. This problem will be discussed further in the next section.

In the future, the successful translocation of even one individual per generation between subpopulations should alleviate the effects of genetic drift on variation and inbreeding depression on fitness. Managers should therefore be able to protect the viability of small isolated populations of selected vertebrates and other species. In addition, managers will need to consolidate some subviable subpopulations by relocating surviving individuals into larger more secure habitat patches. Their goal should be to maintain multiple medium to large subpopulations even at the expense of abandoning some smaller ones. With careful genetic management such natural subpopulations have a reasonable chance of surviving even if $N_e$ falls below 50 locally and 500 over the whole metapopulation.

**CONSERVING EVOLUTIONARILY SIGNIFICANT NATURAL UNITS**

There is an immediate and growing need for more interventive management to conserve tropical biodiversity. In the previous section I presented some arguments for the conservation of genetic variability to maintain population viability. There are two specific management responses to the need to conserve genetic variability. First, individuals in subviable populations can be relocated to safer sanctuaries. This pooling of individuals of diverse geographic origin may enhance local genetic variability. This management technique is now being used in the case of the black rhinoceros,
Diceros bicornis, a species in which many surviving populations number less than 20 individuals. Second, as discussed above, the translocation of individuals can be used to artificially counter the cessation of natural gene flow between subpopulations. Such management practices, involving the relocation or translocation of wild animals, are fraught with difficulties. As noted above, the successful introduction of animals is typically frustrated by both technical and innate biological factors. In this section I will discuss a second problem that may arise as a result of these management policies: namely, the inadvertent mixing of different evolutionarily significant units or species.

There is a danger that translocating individuals can bring together members of different cryptic or sibling species. Despite their ability to mate and produce some apparently viable offspring the hybrids of genetically well-differentiated parents may exhibit reduced fitness and other signs of outbreeding depression (Templeton et al., 1986). Hybridization disrupts locally co-adapted interacting gene complexes and diminishes the viability of the descendant population. This disruption is thought to explain, for example, the increased disease susceptibility observed when normally isolated and disease resistant fish populations are allowed to hybridize. Outbreeding depression, a result of the mating of genetically unrelated individuals, can be thought of as the opposite of inbreeding depression. Like inbreeding depression its likelihood of occurrence and severity are difficult to predict. Similarly, its effects have often gone unrecognized by managers of both captive and free-ranging animals.

The conservation literature has numerous examples of the inadvertent mixing of genetically dissimilar races, subspecies and species. At the outset it must be noted that traditional taxonomy is often a very poor guide to the delimitation of natural taxa or evolutionarily significant units. The classical example of outbreeding depression involves mismanagement of ibex, Capra ibex, in Czechoslovakia: when the local race was extirpated animals of Turkish and African origin were introduced but their hybrids reproduced in the inappropriate season and the population again died out (Robinson and Bolen, 1984; Templeton et al., 1986). Other cases concern captive colonies of several cryptic but chromosomally distinct taxa of spider monkeys, Ateles, owl monkeys, Aotus, and orangutan, Pongo. In many cases it is now clear that such taxa are, in reality, perfectly good biological species and the wasteful hybrid matings are a result of circumstances and inadvertent mismanagement. It is surprising how many allegedly well-known species are in fact so poorly known that mismanagement is almost inevitable. Subspecific taxonomic categories are notoriously poor guides for management decisions. The subspecies taxon has, for example, been abandoned by evolutionary biologists as a useful category as it is rarely congruent with evolutionarily significant units. Subspecies, defined by morphological criteria, may either turn out to be well-differentiated parapatric species or merely poorly marked local races in a continuously variable metapopulation. The distinction is critical to managers as mixing members of different species can negate any conservation program.
Let me illustrate the importance of defining evolutionarily significant units for conservation management with a few Southeast Asian examples. It is not known to what extent gibbons, *Hylobates*, from different areas are genetically compatible. Isolated subpopulations of *H. agilis* from northern peninsular Malaysia, Sumatra and Kalimantan may or may not be genetically compatible. Similarly, the consequences of crossing *H. lar* *carpenteri* from north Thailand with conspecific *H. I. entelloides* from peninsular Thailand or *H. I. vestitus* from Sumatra or *H. I. lar* from peninsular Malaysia are not predictable. No quantified data exist on the fecundity of captive hybrid pairs or the viability of their offspring. Similarly with the Sumatran rhinoceros, the consequences of planned breeding programs (Maguire et al., 1987) incorporating animals from Sumatra, peninsular Malaysia and Sabah are not predictable. These populations have been isolated from each other for at least 10,000 years and, as in the case of the gibbons, their degree of genetic differentiation from one another is still unknown. The same problem exists with tigers: Are traditionally recognized subspecies (*Panthera tigris sumatrae* and *P. t. corbetti*) useful categories for species management (Maguire and Lacy, 1990)? Again, subspecies status is often a poor guide; the montane rats grouped as subspecies of *Rattus alticola* by earlier workers were subsequently shown to be an assemblage of convergent species (Medway and Yong, 1976).

The problem is even worse for groups that are not as well known as mammals. In my studies of medically and economically important molluscs we found that the subspecies of the host snail of the blood fluke, *Schistosoma japonicum*, are actually good species (Woodruff et al., 1988), the three races of the host snail of *S. mekongi* are actually four sibling species (Staub et al., 1990), the 28 recognized species of *Corbicula* clams are actually a single species (Kijviriya et al., in press) and the Thai vectors of *Paragonimus* (*Brotia* and *Paracrostoma*) are not valid genera (Klinhom et al., in prep.). Similarly, with the trematode parasites, we found the subspecific taxonomy of *S. japonicum* to be wrong (Merenlender et al., 1987) and confirmed that *S. malayensis* is a distinct species related to *S. mekongi* not *S. japonicum* (Woodruff et al., 1987).

Managers will obviously need help in defining the limits of evolutionarily significant units if they are to avoid the genetic consequences of inadvertently mixing individuals of different species. They should be aware that the biological species concept has been refined considerably in the last 20 years and that older notions that good species never hybridize have been tempered (Otte and Endler, 1989). The recognition that locally co-adapted gene complexes must be conserved can have a counterintuitive impact on conservation plans; see, for example, Vrijenhoek's (1989) outstanding contribution to the management of the Sonoran topminnow. The consequences of ignoring natural genetic units are now becoming clear in the case of the economically important anadromous Pacific salmon, *Oncorhynchus* sp. (Waples and Teel, 1990). Massive reintroductions of genetically altered (albeit unintentionally), hatchery-raised salmon are compromising long-term fitness and destroying co-adapted gene complexes evolved over
The correct identification and characterization of species and other taxa for management requires the type of data rarely gathered by one person. Once simply the description of obvious phenotypic variation and the application of formal names, systematics now uses a variety of biochemical, multivariate statistical, and other sophisticated approaches in explicit analytical frameworks (e.g. Gould and Woodruff, 1986). Basic to such studies are good natural history observations of life history, ecology, behavior and interactions with other organisms. I applaud the Malayan Nature Society's efforts in stimulating interest in field biology. Nevertheless, it is a fallacy to believe that because we have field guides to some groups of organisms we have enough information to plan for their conservation. Local studies of nature history, published reports of observations in the Malayan Naturalist, and illustrated guidebooks are the essential first steps in the complex process of data acquisition for conservation. Managers are being called on to facilitate the future evolution of species; a formidable task in which traditional taxonomy is often misleading. I join the other participants in this conference and the larger international community of biologists in calling for increased efforts in field biology, natural history and systematics (Greene and Losos, 1988; Wilson and Peter, 1989). Without such renewed commitment to the basics, managers can not be expected to successfully meet the challenges confronting them.

OBTAINING GENETIC INFORMATION FOR WILDLIFE MANAGEMENT

It is only very recently that genetic considerations have become important in species conservation management. It should come as no surprise therefore that existing genetic data bases and techniques for monitoring genetic variation in free-ranging animals are inadequate. Several methodologies are available for assessing different types of genetic variability:

- First, allozyme electrophoresis of blood or other tissues can be used to estimate variation at the level of populations and individuals (Murphy et al., 1990). Such data reflect variation at single structural gene loci and multiple loci surveys of the proportion of loci that are polymorphic (P) and the level of individual heterozygosity (H) are available for about 1000 species of animals. Unfortunately, most species of interest to wildlife managers in Asia have yet to be studied in this fashion. The same limitation applies to more recently developed techniques that examine patterns of nucleic acid variation by restriction site analysis and sequencing (Hillis and Moritz, 1990).
- A second methodology, based on quantitative (polygenic) genetic theory, seeks to assess other kinds of genetic variability that are also important to population viability. Estimates of variation are derived by monitoring traits of moderate to high heritability (such as body length, size of permanent molar teeth, degree of asymmetry in certain bilateral features) in a subpopulation (Lande and Barrowclough, 1987). Such data take several generations to gather and despite their value are still practically non-existent
for free-ranging animals of concern to wildlife managers. Nevertheless, with improved operational utility of quantitative genetic theory we can expect that more attention will be paid to this approach in the future.

- A third type of genetic variation involves relatively large changes in chromosome morphology or number that can be seen in treated cells under a microscope. Such variation has been useful in sorting out some groups of sibling species which differ in chromosome number, centromere position, and changes like inversions and translocations. For example, the Sumatran and Bornean orangutan (Pongo pygmaeus) differ in a pericentric inversion on chromosome 2 (Seuanez, 1986). This methodology, which depends increasingly on tissue culture is of limited use to population managers.

- Finally, the innate genetic load of a subpopulation and probable severity of inbreeding depression can be assessed by large scale breeding experiments. Not surprisingly, this approach to monitoring genetic variation has rarely been applied to free-ranging animals (Lacy, 1991).

These various approaches to monitoring genetic variation in natural populations all have serious limitations. Two require that tissues be collected from living animals and two call for multiple generation breeding or monitoring experiments. In the past, animals were simply killed to obtain tissue samples and other data, but for threatened or endangered species this is no longer acceptable. Today, live trapping is more commonly employed to obtain blood or tissue biopsy samples. Such samples typically require freezing in liquid nitrogen, however, and this presents great difficulties at many field sites and in the transportation of the tissues back to the laboratory. Clearly, none of these methodologies are well-suited to the urgent needs of the wildlife manager.

Ideally, one would like to be able to assess the genetic variability of many individuals at many loci with a very small tissue sample obtained without harming the animals. My students and I have developed a promising new technique of non-invasive tissue acquisition which, when coupled with recent advances in molecular genetics, allows us to overcome some of the problems of existing techniques. We have been able to obtain enough DNA from single plucked or shed hairs and feathers to assess genetic variation at several loci. A selection of nuclear and mitochondrial genes in the hair cell or feather shaft can be amplified several hundred thousand times by the polymerase chain reaction (PCR) using gene specific primers. The amplified products of each gene are then sequenced directly to reveal genetic variation at its most fundamental (base-pair) level. One of the great advantages of our approach is that the tissue can be moved without freezing or preservation.

We are presently conducting pilot studies of selected genes in chimpanzees Pan paniscus and P. troglodytes, gibbons, Hylobates sp., and hornbills (Bucerotidae). Variation in the mitochondrial D-loop (which is maternally inherited) and several nuclear microsatellite loci is high enough to be useful in establishing pedigree relationships. We plan to construct a formal pedigree for the Gombe chimpanzees and establish the relationships among helpers-at-the-nest in brown hornbills, Ptilolaemus tickelli, using these hypervariable loci. More conservative loci like mitochondrial cytochrome-b, for example,
are useful in discriminating between animals of different geographic, racial or subspecific origin. These loci may allow us to establish the geographic origin of individual orphaned gibbons and thus aid in their rehabilitation and reintroduction to appropriate areas. We will publish protocols and preliminary results of these studies in 1991; photographs of gibbon and hornbill genes, and a sequence derived from the latter, are published elsewhere (Woodruff, 1991a).

To demonstrate the utility of our new approach we have also embarked on an attempt to monitor the genetic effects of rainforest fragmentation on small mammal population viability. Specifically, we will conduct population viability analyses of rat, tree shrew, and other small mammals inhabiting rainforest patches of different sizes during the first six years following isolation. These habitat patches were all isolated in 1987 when the creation of the Chiew Larn reservoir flooded a forested valley in the Khlong Saeng Wildlife Sanctuary, Thailand, and created 165 islands (Nakhasathien, 1988, 1989; Wanghongsa, 1989). Demographic changes in selected populations will be monitored by seasonal live-trapping as will levels of genetic variation, inbreeding and gene flow. This study will provide one of the first cases where both genetic and ecological aspects of population viability are monitored in the critical first 20 generations following insularization. In addition, the study promises to contribute to conservation biology in three significant ways. First, the development of the genetic monitoring technique based on non-invasive sampling of DNA from hair will have wide applicability. Second, the demonstration that population viability can be monitored in common small mammals should lead to improved management practices for rarer and more endangered species. Finally, the lessons learned from this study in Thai forest fragments should be applicable to biodiversity conservation elsewhere in the tropics.

**DISCUSSION**

I have argued that the maintenance of genetic variation should be a central theme in plans for the long-term survival of populations. In Malaysia during the next decade, as the size of populations and habitat patches are further reduced, genetic drift and inbreeding will become dominant concerns. Unless more attention is paid to maintaining or increasing genetic effective population sizes ($N_e$) our reliance on small protected areas to sustain viable populations naturally is doomed to failure. Most small and isolated populations cannot sustain themselves naturally. As a consequence there is an urgent need to develop more effective techniques of intervention management. Existing techniques of monitoring genetic variability, translocating individuals and selective culling are inadequate and based on far too few empirical and experimental studies.

Although I have argued that genetic considerations are very important for the long-term survival of populations I emphasize that, in populations on the verge of extinction, genetics is less important than demography. Genetics is unimportant if a population becomes extinct; only when short-term persistence is ensured should genetic concerns receive attention. It is
important to remember that there are very few genetically-defined hopeless cases and that populations can recover from extremely low numbers. Management plans based exclusively on genetic concerns have been rightly criticized and abandoned (Lande, 1988). Management of particular species should be based on both genetic and demographic considerations. Population viability analyses consider both sets of factors simultaneously in seeking to identify and minimize risks.

My argument for increased attention to genetic aspects of conservation can also be criticized for focusing efforts at the levels of populations and species. In doing so, we run a risk of failing to conserve higher levels of organization like communities. Certainly, if we devoted all our efforts to rare and endangered species this may be true (Main, 1982; Hutto, et al., 1988). Given that we cannot save every threatened species I believe the best compromise is to identify and conserve selected key-stone mutualists and umbrella species whose survival will ensure the persistence of whole communities (Woodruff, 1989, 1991a). Colwell’s (1989) principle of relative replaceability is also useful in choosing from among the many species requiring urgent attention. Conservation biologists should not devote all their energies to last resort cases.

Finally, my call for greater interventive management of natural populations may offend those who believe in ideals of wilderness and freedom. I am convinced that in all but the largest reserves our traditional laissez faire approach to wildlife management will fail us. The “altered states” in which most animals find themselves today are characterized by declining Ne and increasing human impacts. Under such circumstances Nature will no longer serve us as the steward of biodiversity; instead, intensified natural and artificial selection, genetic drift and inbreeding will constitute Nature’s predictable response and local extinction the predictable outcome. As Wallace and Darwin showed, selection is both the main agent of creative evolution and of extinction. Our activities have already altered the selective regimes experienced by most living organisms and the old dichotomy of natural versus artificial selection is increasingly false. I therefore see little need to apologize for advocating management practices that will further alter certain regimes of natural and sexual selection. If biodiversity conservation is our goal then we have few options but to use selection as a management tool. The distinction between natural and artificial selection is already completely blurred in cases where extirpated populations have been reintroduced after periods of intensive ex situ care. Only when humans accept responsibility for managing the levels of selection operating on the populations, species and communities threatened by their activities can we again reach a state of being in harmony with nature.

ACKNOWLEDGEMENTS

Participation in the International Conference on Tropical Biodiversity “In Harmony with Nature” sponsored by the Malayan Nature Society was made possible by a grant from the U.S. National Science Foundation. I appreciate the Society’s invitation and the assistance of Peter Ashton,
Warren Brockelman, S.G. Tan, H.S. Yong and David Wells. My research is funded by grants from the U.S. Agency for International Development, the U.S. National Science Foundation, the U.S. National Institutes of Health, and the Academic Senate of the University of California.

REFERENCES


Klinhom, Us, D.S. Woodruff & E.S. Upatham. Genetic variability among some Thiariidae (Mesogastropoda: Mollusca) of Thailand. In prep.


