
3 Conservation genetics and conservation biology: a troubled marriage

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ABSTRACT

In two prophetic papers, Otto Frankel presented the conceptual and moral agenda for the discipline of conservation genetics. Within the last decade the penetration of genetics into species-level conservation programs has been accomplished, completing the first phase of the field's development. Simultaneously, population genetics, demography, and population ecology have presented new approaches to the estimation of minimum viable populations; these estimates have increased by orders of magnitude, presenting conceptual and political problems to conservationists. In addition, we are seeing a growing hostility to both genetical and species-level programs in favor of so-called ecosystem approaches. We argue that the species – ecosystem dichotomy is a false one, though it will lead to a more integrated synthesis of conservation theory and practice.

A GLANCE BACKWARD

The chapters in this section constitute an authoritative status report on conservation genetics. Instead of presenting a summary of these summaries, we first tip our hats, as it were, to the people and events that helped shape the present, and second, peer ahead at some looming controversies. Some of these controversies could jeopardize our mission to protect genetic and biological diversity.

Until the middle 1970s, most of the people in charge of conservation ignored genetics, and most of the people in charge of genetics ignored conservation. But beginning around 1970, plant geneticists started to become alarmed about the disappearance of primitive or traditional crop varieties and their replacement by modern, genetically uniform, cultivars. Geneticists suspected then as they do today that the seeds of the green revolution contained the agents of their own ultimate collapse, namely, genetic uniformity. They began to question the wisdom of discarding, in a single human generation, the products of thousands of

years of artificial selection for adaptation to microhabitat diversity, and for resistance to stress and drought, disease, and attacks by pests.

Several publications appeared in the early seventies that called for or contained protocols for the sampling and maintenance of germ plasm collections (Bennett 1965; Frankel and Bennett 1970; Marshall and Brown 1975; Frankel and Hawkes 1975; see Frankel and Soulé 1981 for further citations). An international system of gene banks was endorsed by the United Nations Conference on the Human Environment in Stockholm, 1972. The International Board of Plant Genetic Resources (IBPGR) was established within the Food and Agriculture Organization of the United Nations in the same year in order to further the collection, conservation, documentation, and use of germplasm for crop species (Williams 1988). Plant geneticists, we can now see with hindsight, knew that sustainable agroecosystems were impossible without genetic, as well as species diversity. Today, a fairly sophisticated, global system of economic plant germ plasm collections is assembled.

In 1970 and 1974, Otto Frankel, the prophet of conservation genetics, published two landmark papers (Frankel 1970, 1974). In the second paper entitled "Genetic conservation: our evolutionary responsibility" he issued a challenge to the field of genetics, a rather unusual one too, in that it was basically ethical. To quote him (1974), "... genetics has social responsibilities in two directions: first to collaborate in planning the biological system of conservation so as to establish the highest possible evolutionary potential; second, to help in establishing an evolutionary ethic, as part of our social ethics, which will make it acceptable and indeed inevitable for civilized man to regard the continuing existence of other species as an integral part of his own existence. This demands continuing evolution." Frankel

(1974) also foresaw the need for pervasive management of nature, noting that "[wild] species almost everywhere in the world will depend on organized protection for their survival" and such protection is predicated on management that facilitated "continuing evolution."

Frankel (1974) asked the important questions, including what were the conditions for continuing evolution. "The prime parameters," he said, "are the level and distribution of variation, the size of the **minimum viable population** (emphasis ours), and the optimal and minimal sizes of reserves. We need to know the minimum population size which is likely to yield a required level of variation." Harlan (1975) made a similar statement soon thereafter, and *in situ* conservation of traditional crop germplasm has been promoted more recently (e.g. Wilkes 1983; Nabhan 1985; Altieri and Merrick 1988). Soon thereafter, zoologists (Flesness 1977; Denniston 1978; Seal 1978) were to sound the alarm about the impact of genetic drift and bottlenecks on the amount of genetic variation in small, isolated, natural populations, although at that time there was little published data confirming these theoretical expectations.

As evidence for effects of genetic drift, Frankel cited our own work on island lizards (Gorman et al. 1975; Soulé 1980) that demonstrated the "small island effect." Lizard populations on islands smaller than five or ten hectares have lower than normal levels of heterozygosity. Based on these data, Frankel (1974) quotes Soulé (personal communication) as concluding that minimum population sizes assuring long-term survival (thousands of years) should be of the order of 10^4 or more, a number derived from the estimated population size of island lizard populations having levels of genetic variation typical of those of related mainland populations.

Frankel anticipated a controversy known later as the SLOSS debate among biogeo-

graphers and ecologists — the relative benefits of **Single Large Or Several Small** conservation units. He noted that "It has been argued that population subdivision maximizes the potential rate of evolution But it will be rash to conclude that many small reserves are more effective than fewer larger ones." Indeed, the subsequent discovery that persisting species in isolates are distributed as nested subsets (i.e. the species that persist in small patches are virtually always a sub-set of those persisting in larger patches, and those that disappear in small patches are virtually the same set from patch to patch), argues for larger reserves. This predictability in patterns of extinction has confirmed the advantages of large protected areas for some taxa (Patterson and Atmar 1986; Blake 1991; Bolger et al. 1991).

Frankel did not eschew philosophy either. Elaborating on the need for an ethical stance in genetics, Frankel came close to embracing a version of the intrinsic value argument for conservation. He asks if it is not our responsibility to keep evolutionary options open, so far as we can, for the sake of future humans? He went further in the direction of extending the ethical community to non-humans, hoping that this idea of evolutionary responsibility would deepen into an ethic "if and when men come to regard other species as an essential part of their own existence." This latter view expresses a concept of "self" that includes identifications with non-human species, and is not far from the deep ecology philosophy as enunciated by Arne Næss (1989, this volume).

The first international meeting concerning the application of conservation genetics to wild species occurred at a conference in La Jolla, California in 1978. The results of that conference (Soulé and Wilcox 1980) produced the first specific recommendations about genetical MVPs for animals, including the 50/500 numbers (effective population sizes) for short-term and long-

term programs, respectively (Franklin 1980; Soulé 1980; Frankel and Soulé 1981; Hedrick and Miller this volume). An effective size of 50 was thought to provide some protection against short-term loss of fitness due to inbreeding; an effective size of 500 was thought to prevent loss of genetic variation, *per se*. These rules of thumb have fallen into disrepute for several reasons. First, they are based solely on genetical argumentation and data; since their publication in 1980, other fields, including demography and population ecology have started to advance their own recipes for the estimation of MVPs (Shaffer 1981; Soulé 1987). Nowadays, MVPs usually are based on assumptions or objectives about the probability of persistence (say 0.95) and time intervals (say 200 years). Some recent MVPs incorporate population, environmental, as well as genetical considerations (e.g. Gilpin 1989; Doak 1989).

Second, these numbers have been misused more often than they have been applied correctly. As pointed out by Harris and Allendorf (1989), many practitioners have ignored the difference between census size and effective size, thus grossly underestimating the actual MVP, especially for long-term conservation purposes.

Third, and related to the first point, it is currently fashionable to denigrate the significance of genetics in the estimation of MVPs, on the grounds that the effects of environmental variability on population persistence (Goodman 1987a; Belovsky 1987) will swamp any impact that inbreeding and loss of genetic fitness might have (Schwartz et al. 1986; Dawson et al. 1987; Lande 1988; see also Pimm et al. 1988, 1989). This conclusion, in our opinion, is premature (see below).

Just as it does in most other cultural phenomena, the pendulum in science swings back and forth. Thus, the current unpopularity of genetics is neither unprecedented nor unexpected. In the past, many conser-

vationists have been extremely reluctant to accept the role of genetics in conservation. The reasons are not difficult to discern, and they had nothing to do with science, *per se*. Genetics is an arcane field, in part because of its difficult jargon, and in part because it is quantitative. It kindles fear in many biologists and laypersons alike, and fear creates hostility. Second, genetics is associated with theories of racial differences, human instincts, and similar deterministic ideas that were anathema to many left-leaning intellectuals during the middle decades of this century. Only recently has the role of genetics in human psychology, physiology, and disease been tolerated once more (e.g. Bouchard et al. 1990).

Another reason for the reluctance of some to accept the role of genetics in conservation is that acceptance would have meant the abandonment of cherished practices. In the zoo world, for example, many curators wished to maximize the number of species in their respective collections. A result was competition for species diversity; group sizes for many species were commonly in the range of two to six individuals; rarely were there interchanges between zoos. To acknowledge that inbreeding might be a factor in the frequent loss of these small groups would have necessitated the abandonment of many species in favor of larger population sizes for those retained. It took the encouragement of a few leaders (Benirschke et al. 1980; Conway 1986) and the inspired work of Katherine Ralls, Jon Ballou and their colleagues (Ralls and Ballou 1983; Ralls et al. 1988), not to mention the growing governmental red tape and economic costs of replacing lost groups, to convince many zoo curators that inbreeding was a leading cause of group morbidity and extinction.

The role of genetics in nature conservation was consolidated by the publication of two books (Frankel and Soulé 1981; Schonewald-Cox et al. 1983). In the latter vol-

ume, Frankel (1983) reiterated that a central concept of conservation genetics is fitness. These days when we ask such questions as (1) why do we census for heterozygosity?, (2) why do we calculate effective population size (N_e)?, (3) why do we do pedigree analysis?, (4) why do we do molecular genetic studies?, the answers are usually framed in terms of (1) either minimizing the loss of genetic variance which is thought to be associated with fitness, (2) minimizing the costs of inbreeding, or (3) avoiding trans-specific crosses between morphologically similar species. Conservation genetics exists for one reason only – to promote the fitness of targeted populations (e.g. Ralls and Ballou 1986). This is our commandment.

Conceptually, though, fitness is not as straightforward as it might seem. The concept of fitness is often dichotomized – always a danger sign in biology. The first category is immediate or short-term fitness, such as the average viability or fecundity of individuals living now. This kind of fitness is easy to define operationally and is relatively easy to measure. The second category is "potential" fitness. It represents the idea that genetic variation in a lineage is required to adapt, through natural selection, to changing conditions. It is based on the premises that (1) genetic variation can be limiting, and (2) any loss of genetic variation can compromise the future capacity of a population to adapt and survive. Long-term fitness, as represented by genetic variation, is like wealth, as represented by gold coins buried in the garden. It is a hedge against future disasters.

Potential **anything** is problematic, and potential or long-term fitness is no exception. First, it is a different kind of concept altogether from short-term fitness, because, unlike gold, there may not be a straightforward relationship between genetic variation and wealth. Whereas it may be assumed that two pieces of gold will buy twice as

many pigs as a single piece, there is no guarantee that a population with 8 % heterozygosity has twice the probability of surviving 1,000 years as one with 4 % heterozygosity. Nevertheless, a proportionality between genetic variation and persistence time (long-term fitness) is assumed; this idea could be expressed as follows:

$$E_t \approx A [V_A]$$

where E_t is the expected time of persistence of a population, A is a species-specific constant representing general "adaptiveness," and V_A is the current level of additive genetic variation. The evidence for such a relationship is remarkably thin, being limited to a few short-term studies (Frankel and Soulé 1981). Nevertheless, much of what we call conservation genetics is based on this premise.

IS GENETICS RELEVANT TO POPULATION PERSISTENCE?

As already mentioned, genetics has lost its short-lived hegemony in the MVP arena for natural populations. Will the pendulum ever swing back, or is conservation genetics banished to the computers of those managing gene banks, captive groups in zoos, and botanical gardens? This leads us to the subject of persistence, *per se*, and our ability to predict it.

The issue of population persistence or viability is intellectually fascinating, in part because it requires a multidisciplinary, systems approach (Gilpin and Soulé 1986). Consider a population restricted to a patch of habitat; assume there is negligible immigration. Given that one knew enough about this population's demography, its environment, and the relationships between the two, one could, at least in theory, estimate

the mean and variance of its persistence time (Goodman 1987a; Belovsky 1987). In spite of the complexity and elegance of such an analysis, however, the result could be very misleading.

At least two factors would have been left out. One of these is the possibility of a catastrophe (Ewens et al. 1987); we won't elaborate on this subject here. The other factor is the interplay between population dynamics and the loss of fitness due to inbreeding or genetic drift (Soulé 1987). Returning to the population mentioned above, could it persist at a small size (say, $N \leq 50$) long enough to lose about 10 % of its genetic variation? If it could, would this amount of genetic attrition produce detectable and ecologically significant impacts on the fecundity and viability of its members? For example, Frankel and Soulé (1981: p. 68) predicted on the basis of laboratory results with domesticated animals and plants that a 10 % increase in the inbreeding coefficient is often likely to produce a 10 to 25 % lowering of total reproductive performance. It has been suggested that reproductive depression of this magnitude could significantly compromise r , the intrinsic rate of increase, thus compromising a small population's ability to persist in a fluctuating environment (Soulé 1987).

Simulating the effects of inbreeding

One of us (LSM) is exploring this question by simulating the impact of inbreeding on population growth. Only a brief overview of preliminary results are presented here. Consider two small, recently isolated populations with three age classes and no density dependence. One has an r near zero, but positive (approximately 0.06), a reasonable rate for many natural mammal populations; the other has an r of approximately 0.75, near the high end observed for mammals in the wild (Pianka 1970; Robinson and Redford 1986). The demographic costs of in-

breeding on survivorship and fecundity may be obtained from the literature (e.g. Ralls et al. 1988). These costs may then be incorporated into a Leslie matrix growth model by weighting survivorship and fecundity by the fitness reduction due to inbreeding. For example, p_x (survivorship during age x) values are replaced by $p_x(F,t)$, where F is the average inbreeding coefficient for individuals born during time period t , and m_x (fecundity at year x) values are replaced by $m_x(F,t)$, age-specific reductions in these parameters due to inbreeding. In essence then, age-specific demographic values are reduced according to empirically measured inbreeding costs at each age. Based on the modified values of survivorship and fecundity, the constant Leslie matrix L is replaced by a variable matrix $L(F,t)$, which can be projected to estimate population sizes in the future.

The results of two such population projections are shown in Figures 1 and 2. Both are initiated with a population of 30; four projection intervals (years) are shown. The population with $r = 0.06$ (Figure 1) grows to over 40 in four years with no inbreeding effects. With inbreeding, however, the population declines to 15. For the population with a very high intrinsic rate of increase, the size reached in four years is large, even with inbreeding costs, but it is less than half that of the same population without inbreeding costs (Figure 2).

As mentioned, it is currently fashionable to dismiss the role of inbreeding depression when projecting the viability of small populations. Some experts (Schwartz et al. 1986; Dawson et al. 1987; Lande 1988; see also Pimm et al. 1988, 1989) argue that when a population is so small that its fitness may be compromised by inbreeding, that it is in much greater danger of crashing from demographic and environmental stochasticity. And such a population, they argue, is unlikely to persist long enough to experience enough inbreeding to do it significant

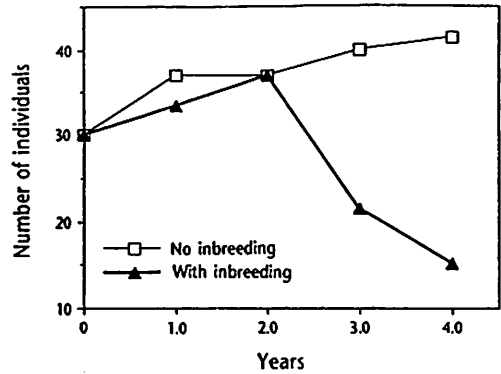


Figure 1. The effect of imposing an inbreeding depression cost on a population with a low but positive intrinsic growth rate ($r_m = 0.06$) typical of mammalian species in nature. The model is a deterministic Leslie Matrix based on a population with two age classes. See text.

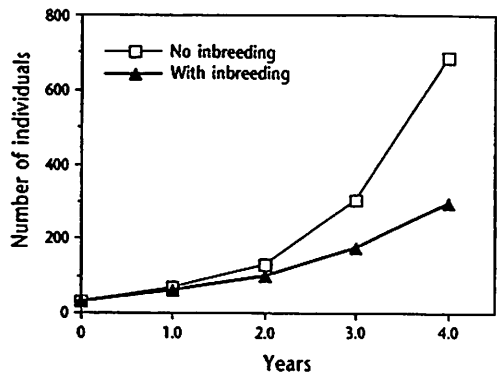


Figure 2. The effect of imposing an inbreeding depression cost on a population with a very high intrinsic growth rate ($r_m = 0.75$). The model is a deterministic Leslie Matrix based on a population with two age classes. See text.

damage. We believe, to the contrary, that theoretical and empirical studies such as the one just summarized will demonstrate that inbreeding can affect population size, and therefore persistence, in the face of random demographic events and environmental fluctuations.

Current simulation studies in collabora-

tion with Peter Smouse at Rutgers University are incorporating age-specific costs of inbreeding as variables in a stochastic population growth model (L. S. Mills and P. Smouse, in preparation). In addition, LSM is testing the implications of the model using natural populations of the California red-backed vole (*Clethrionomys californicus*) in forest remnants.

MVP HYPERINFLATION

The second problem we would like to mention derives from the success of conservation biology as reflected in the startling changes in the last 25 years. Recall that in the sixties, MVPs (demographic) were in the range of 25 to 50 (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972). A population larger than this is not much threatened by demographic stochasticity (Leigh 1981; Goodman 1987a). The next stage in MVP studies, the genetic era, could be characterized by the 50/500 criteria. The 500 number refers to a genetically effective size of 500, which often translates to a census size of 2,000 to 5,000 or more (Nei and Graur 1984; Harris and Allendorf 1989; Michael Smith, personal communication; R. Frankham, personal communication). Then came the era of MVP hyperinflation, with values in the range of 10^4 to 10^6 based on analyses of persistence based, in turn, on the effects of random environmental fluctuations on the dynamics for single populations (Goodman 1987a; Belovsky 1987). (Note that the numerical criteria used for germplasm collections is not covered in this discussion.) These large numbers, however, are problematic for both pragmatic and scientific reasons. The pragmatic problem is that administrators and managers are confronted with unreachable population targets; to follow expert advice in many cases would not be economically or politically expedient. Consider, for exam-

ple, the home range of a mountain lion (*Felis concolor*) in North America may be 100 km^2 or more (Hempker et al. 1984; Hopkins et al. 1986). If the MVP is 10^5 , a viable population in the USA would require more than all the land in the contiguous 48 states.

In the United States, let alone in nations where wildlife is competing for space with many landless or poor, only a very single-minded conservationist would stand up in public to argue that an area of these dimensions be given back to nature. But neither should we disguise the truth as we see it. How do we escape from this dilemma? The only answer, we believe, is to accompany the arguments for such huge numbers with practical management alternatives. Among these would be (1) the establishment or enhancement of multiple populations, (2) a combination of *in situ* and *ex situ* approaches, including the storage of germplasm (e.g. seed banks, tissue culture, cryopreservation of sperm, embryos, and larvae), and even, at some risk to the species, (3) accepting proposals that buy time instead of achieving an ideal solution in one step.

Finally, an MVP in the range of 10^5 to 10^6 may not be defensible on purely biological grounds (Soulé 1987; Goodman 1987b) for the simple reason that a single, very large population is neither the prudent strategy nor the natural solution. The total number needed may be much less if the individuals are living in two or more places, the environments of which are not perfectly correlated. In nature, many species are distributed as metapopulations – a patchwork of interacting populations over a wide and heterogeneous geographic region; at any given time some of the patches are extinct and some are newly colonized. Partly as a consequence of the environmental differences that these manifold, dispersed population units encounter, the persistence of a metapopulation of a given N or N_e is ex-

pected to be superior to that of a single population of the same numerical order (Soulé 1987; Goodman 1987b; Gilpin and Hanski 1991). It seems probable, therefore, that the incorporation of both spatial and temporal heterogeneity along with metapopulation dynamics into MVP analysis will reduce the number of individuals required to ensure long-term viability. Metapopulation dynamics could either increase or decrease the rate of loss of genetic variation, however, depending on the extinction and recolonization rates (Gilpin 1987), as well as the population growth rates.

THE "FAILURE" OF SPECIES CONSERVATION

Another potential cloud on the horizon is the growing reaction against species-based conservation. More and more these days, we hear voices raised against the emphasis on species rather than on habitat, ecosystem, or landscape approaches (e.g. Harris 1984; Scott et al. 1987; Simberloff 1987; Kohm 1991). Because conservation genetics is inherently a species or population-based discipline, conservation genetics is guilty by association with so-called species chauvinists.

The anti-species movement could produce a backlash against endangered species and the scientists and managers who work to protect them. The tendency among some conservation biologists to dichotomize nature into species and ecosystems almost guarantees that many innocent species and dedicated scientists and professionals will be characterized as "bad guys." The new heroes are the plant geographers, the ecosystem ecologists, restoration ecologists, and landscape ecologists who favor a more holistic, comprehensive and proactive conservation strategy.

The growing backlog of endangered species

It is easy to see why many people are becoming frustrated, indeed infuriated with species-based conservation. Consider the statistics on endangered species in the US. There are about 570 officially listed threatened and endangered species, but only about half of these have recovery plans. Recovery plans establish the criteria for recovery and recommend the management interventions that should be implemented. But these plans have no teeth. No funds accompany the approval of recovery plans, and rarely do the plans identify critical habitat, let alone protect it. In fact, most plans are nothing more than a promise cloaked in a prayer. Granted, the provisions of the Endangered Species Act prohibit the so-called "taking" of individuals or the destruction of its habitat, but a determined developer can often find a way to circumvent the recommendations in a recovery plan.

These problems of implementation and enforcement, however, are not the only reasons for the growing hostility to species-based approaches. Even if recovery plans were efficient and well funded, this strategy would still be unpopular. One excuse for attacking the species approach is that many of the species that receive special attention are large and attractive, ignoring many species-rich groups such as plants and insects (Wilson 1988). Another reason for the growing concern is that species are listed more slowly than they are nominated, and the backlog increases yearly. In the US, there are now more than 4,000 candidate species. Recovery and delisting of species are rare, and recovery plans are produced and implemented at a much slower rate than species are nominated and listed. Many people are now saying that the system has broken down (Scott et al. 1991).

Endangered species are symptoms, not causes

There are other problems. A question asked by growing numbers of conservationists throughout the world is "what is the point of adding a name to a list of moribund species if little or nothing is being done to counteract the causes that produce so many species crises?" These causes are all too familiar: (1) the loss and disturbance of habitat, (2) the fragmentation of habitat, (3) air and water pollution, (4) the spread of exotic species and diseases, (5) climate change, and (6) overexploitation of populations.

Simply put, **the species approach to conservation is a crisis management approach** (Salwasser 1991). Even those activists who are successful in obtaining funding for their favorite endangered species may perceive the futility of trying to rescue a particular taxon where nothing is being done to prevent many more species from becoming endangered. Of course, endangered species are very popular, and organizations can raise a lot of money for them, but the supporters of less popular species or of whole systems are frustrated when millions of dollars are spent on a few flagship species, leaving little or nothing for less charismatic creatures, nor preventing further environmental deterioration.

IN DEFENSE OF PLURALISM

We are concerned, though, that the conservation crisis could evolve into a very destructive conflict. On the one side are the species enthusiasts who generally defend large, charismatic vertebrates and keystone species; on the other side are the ecosystem enthusiasts who favor a habitat approach based on (1) the identification, classification, and protection of representative sam-

ples of all biotic communities (e.g. Jenkins 1988; Huntley 1988; Crumpacker et al. 1989) and (2) the management of these protected areas at the appropriate physical and temporal scales (Clark and Harvey 1988). In theory, there should be no conflict. Just as assessment of impacts at the ecosystem level must depend on the monitoring of individual species (Van Horne 1983), so the conservation of species requires attention to ecosystem processes and disturbance dynamics.

In practice, though, supporters of a species approach are not convinced that a habitat approach can be implemented and maintained for many decades or centuries, particularly in the many parts of the tropics; the list of protected areas that are being overrun, overexploited or destroyed by mining, agriculture, forestry and water projects is growing at an alarming rate, according to the Threatened Parks Register of the International Union for Conservation of Nature and Natural Resources' Commission on National Parks and Protected Areas. Thus, while supporters of systems approaches see money being "wasted" on a few charismatic vertebrates, the supporters of endangered species and captive propagation point to the increasing rate of park failure and the need for a backup system that is more secure, even if less natural.

A naive expression of the ecosystem approach is one that holds the extremist assumption that design and management of protected areas can ignore species altogether, focusing instead on ecosystem processes and patch dynamics. Clearly, though, ecosystem management must attend to the viability of certain, critical species, even if they are not yet endangered. Any protected area will undergo biotic collapse unless designers and managers understand the natural history and viability of certain species. A corollary of this premise is that the failure to manage or maintain these species will

lead to the collapse of the system, or at least to a significant reduction in species richness (Frankel and Soulé 1981; Botkin 1990).

Table 1 presents three sets of questions that may clarify this point. The first question is the amount of area needed to prevent the loss of biological diversity in the system. Strictly speaking, ecosystem approaches do not explicitly identify this question, nor can they approximate a general answer or identify the criteria that should be considered. A biologically defensible solution must be based in part on the minimum genetical and spatial requirements of certain, strongly interacting, species (L. S. Mills and M. E. Soulé, in preparation). For example, if trees of the genus *Ficus*, invertebrates such as starfish or termites, fishes such as groupers, or vertebrates such as beavers, tapirs, alligators or elephants are important in the long-term maintenance of habitat diversity

in the system, special attention must be devoted to the needs and viability of their populations within the protected area or the system of protected areas. The point is that in most places, **system viability cannot be disassociated from species viability.**

A related point is that the fragmentation of wildlands will usually threaten elements of biodiversity that depend on long-range dispersal movements, migratory movements, or foraging movements. Some of these species may be important mutualists (e.g. pollinators, mycorrhizal fungi). For example, if bats are important pollinators of many tree species, it will be necessary to insure that their roosting and breeding sites are protected within the system of protected areas, and that human activities around and in the reserves do not compromise their long-term viability. If deep forest birds or sphingid moths must migrate between wet-

Table 1. Some questions for the designers and managers of protected areas that demonstrate the roles of species and process management in an integrated, "ecological" approach to conservation.

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1. How much area is needed to prevent the loss of biological diversity in the system?
 - What constitutes a substantial loss of biodiversity for the system?
 - What criteria can be used to predict whether such losses will occur?
 - Does the system contain viable populations of all the strongly interacting ("keystone") species? How large an area is needed for these viable populations?
 - Is the system sufficient in size and topographic heterogeneity to generate an appropriate level of disturbance to maintain the necessary diversity of habitats under foreseeable changes in climate and other conditions?
 2. What sensitive species or processes are threatened by loss of connectivity?
 - Would the loss of any species (e.g. mutualist or migratory species) lead to extinction cascades and compromise biodiversity?
 - What interventions or new design features would mitigate such threats?
 3. What management interventions will be needed to prevent the spread of deleterious exotic species?
 - What plants, animals, pathogens are contributing to habitat changes, to decreases in the diversity of native species and assemblages, and to deleterious edge effects?
 - How will these species and changes compromise the viability of critical species or processes?
 - How can these deleterious species and changes be managed/controlled?
-

season and dry-season sites (Karr 1982; Janzen 1986), conservation corridors may have to be established.

The third question in Table 1 points to another category of species – those that are harmful to system stability and species richness. Many of these deleterious species will be exotics, often but not always originating in other continents (e.g. Soulé 1990). Exotic or expanding species of plants, predators, herbivores, or nest parasites (such as cowbirds in the US) often create the conditions for wildfire, for the invasion of weeds, for the mortality of critical pollinators or seed dispersers, for the spread of disease, and the inviability of sensitive species. Management protocols tailored to specific species are a necessity for most such situations.

In conclusion, the design and management of conservation areas will rarely succeed without attending to the needs and control of critical or problem species. The species vs. ecosystem dichotomy, like almost every other dichotomy in biology, is fatally flawed conceptually and operationally. A pure ecosystem approach is just as contradictory as a pure species approach. As we write, the popularity of genetical and species approaches to conservation is waning. So-called holistic approaches are in the ascendancy. To the extent that these trends bring about a biologically realistic synthesis, they are welcomed. A purely genetic approach to population viability is absurd (Frankel and Soulé 1981). A conservation strategy blind to anything except species on the brink of annihilation is absurd. The danger is that the pendulum could swing too far in the other direction. The deep-seated antagonism against genetics, and the hostility that sometimes exists between ecosystem ecologists and species-oriented biologists could undermine the emergence of new, synthetic approaches and technologies.

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LITERATURE CITED

- Altieri, M. A. and L. C. Merrick. 1988. Agroecology and in situ conservation of native crop diversity in the Third World, pp. 361–369. In: E. O. Wilson (ed) *Biodiversity*. National Academy Press, Washington, DC.
- Belovsky, G. E. 1987. Extinction models and mammalian persistence, pp. 35–58 In: M. E. Soulé (ed) *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Benirschke, K., B. Lasley and O. Ryder. 1980. The technology of captive propagation, pp. 225–242. In: M. E. Soulé and B. A. Wilcox (eds) *Conservation Biology: An Evolutionary – Ecological Perspective*. Sinauer, Sunderland, MA.
- Bennett, E. 1965. Plant introductions and genetic conservation: genecological aspects on an urgent world problem. *Scottish Plant Breeding Station Record*: 27–113.
- Blake, J. G. 1991. Nested subsets and the distribution of birds on isolated woodlots. *Conserv. Biol.* 5: 58–66.
- Bolger, D. T., A. C. Alberts and M. E. Soulé. 1991. Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. *Amer. Nat.* 137: 155–166.
- Botkin, D. B. 1990. *Discordant Harmonies: A New Ecology for the Twenty-First Century*. Oxford University Press, Oxford.

- Bouchard jr., T. J., D. T. Lykken, M. McGue, N. L. Segal and A. Tellegen. 1990. Sources of human psychological differences. The Minnesota study of twins reared apart. *Science* 250: 223–228.
- Clark, T. W. and A. H. Harvey. 1988. Management of the greater Yellowstone ecosystem: an Annotated Bibliography. Northern Rockies Conservation Cooperative: 52 pp. P.O. Box 2705, Jackson, WY 83001.
- Conway, W. 1986. The practical difficulties and financial implications of endangered species breeding programs. *Int. Zoo Yearb.* 24/25: 210–219.
- Crumpacker, D. W., S. W. Hodge, D. Friedley and W. P. Grepp. 1988. A preliminary assessment of the status of major terrestrial and wetlands ecosystems on federal and Indian lands in the United States. *Conserv. Biol.* 2: 103–115.
- Dawson, W. R., J. D. Ligon, J. R. Murphy, J. P. Myers, D. Simberloff and J. Verner. 1987. Report of the scientific advisory panel on the spotted owl. *Condor* 89: 205–229.
- Denniston, C. 1978. Small population size and genetic diversity. Implications for endangered species, pp. 281–290. In: S. A. Temple (ed) *Endangered Birds: Management Techniques for Preserving Threatened Species*. University of Wisconsin, Madison, WI.
- Doak, D. 1989. Spotted owls and old growth logging in the Pacific Northwest. *Conserv. Biol.* 3: 389–396.
- Ewens, W. J., P. J. Brockwell, J. M. Gani and S. I. Resnick. 1987. Minimum viable populations size in the presence of catastrophe, pp. 59–69. In: M. E. Soulé (ed) *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Flesness, N. R. 1977. Gene pool conservation and computer analysis. *Int. Zoo Yearb.* 17: 62–68.
- Frankel, O. H. 1970. Variation – the essence of life. *Proc. Linn. Soc. New South Wales* 95: 158–169.
- Frankel, O. H. 1974. Genetic conservation: Our evolutionary responsibility. *Genetics* 78: 53–65.
- Frankel, O. H. 1983. The place of management in conservation pp. 1–14. In: C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde and W. L. Thomas (eds) *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Benjamin/Cummings, Menlo Park, CA.
- Frankel, O. H. and E. Bennett (eds) 1970. *Genetic Resources in Plants*. IBP Handbook No. 11. Blackwell Scientific Publications, Oxford.
- Frankel, O. H. and J. G. Hawkes (eds) 1975. *Crop Genetic Resources for Today and Tomorrow*. International Biological Programme 2. Cambridge University Press, Cambridge.
- Frankel, O. H. and M. E. Soulé. 1981. *Conservation and Evolution*. Cambridge University Press, Cambridge.
- Franklin, I. R. 1980. Evolutionary change in small populations, pp. 135–149. In: M. E. Soulé and B. A. Wilcox (eds) *Conservation Biology: An Evolutionary – Ecological Perspective*. Sinauer, Sunderland, MA.
- Gilpin, M. E. 1987. Spatial structure and population vulnerability, pp. 125–140. In: M. E. Soulé (ed) *Viable Populations for*

- Conservation*. Cambridge University Press, Cambridge.
- Gilpin, M. E. 1989. Population viability analysis. *Endangered Species Update* 6(10): 15–18.
- Gilpin, M. E. and I. Hanski. 1991. *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, San Diego.
- Gilpin, M. E. and M. E. Soulé. 1986. Minimum viable populations: Process of species extinctions, pp. 19–34. In: M. E. Soulé (ed) *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer, Sunderland, MA.
- Goodman, D. 1987a. The demography of chance extinction, pp. 11–34. In: M. E. Soulé (ed) *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Goodman, D. 1987b. How do any species persist? Lessons from conservation biology. *Conserv. Biol.* 1: 59–62.
- Gorman, G. L., M. E. Soulé and S. Y. Yang. 1975. Evolutionary genetics of insular Adriatic lizards. *Evolution* 29: 52–71.
- Harlan, J. R. 1975. Our vanishing genetic resources. *Science* 188: 618–622.
- Harris, L. D. 1984. *The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity*. University of Chicago Press, Chicago.
- Harris, R. B. and F. W. Allendorf. 1989. Genetically effective population size of large mammals: an assessment of estimators. *Conserv. Biol.* 3: 181–191.
- Hedrick, P. W. and P. Miller. 1992. Conservation genetics: theory and management of captive populations. This volume.
- Hempker, T. P., F. G. Lindzey and B. B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. *J. Wildl. Mgmt.* 48: 1275–1284.
- Hopkins, R. A., J. J. Kutilek and G. L. Shreve. 1986. Density and home range characteristics of mountain lions in the Diablo Range in California, pp. 223–235. In: S. D. Miller and D. D. Everett (eds) *Cats of the World: Biology, Conservation, and Management*. National Wildlife Federation, Washington, DC.
- Huntley, B. J. 1988. Conserving and monitoring biotic diversity: some African examples, pp. 248–260. In: E. O. Wilson (ed) *Biodiversity*. National Academy Press, Washington, DC.
- Janzen, D. H. 1986. The eternal external threat, pp. 286–303. In: M. E. Soulé (ed) *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer, Sunderland, MA.
- Jenkins, R. E. 1988. Information management for the conservation of biodiversity, pp. 231–239. In: E. O. Wilson (ed) *Biodiversity*. National Academy Press, Washington, DC.
- Karr, J. R. 1982. Avian extinction on Barro Colorado Island, Panama: A reassessment. *Amer. Nat.* 119: 220–239.
- Kohm, K. A. (ed) 1991. *Balancing on the Brink of Extinction: The Endangered Species Act and Lessons for the Future*. Island Press, Washington, DC.

- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241: 1455–1460.
- Leigh, E. G. jr. 1981. The average lifetime of a population in a varying environment. *J. Theor. Biol.* 90: 231–239.
- MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Marshall, D. R. and A. H. D. Brown. 1975. Optimum sampling strategies in genetic conservation, pp. 53–80. In: O. H. Frankel and J. G. Hawkes (eds) *Crop Genetic Resources for Today and Tomorrow*. International Biological Programme 2. Cambridge University Press, Cambridge.
- Nabhan, G. B. 1985. Native crop diversity in Aridoamerica: Conservation of regional gene pools. *Econ. Bot.* 39: 387–399.
- Næss, A. 1989. *Ecology, Community and Lifestyle*. Cambridge University Press, Cambridge.
- Næss, A. 1992. Sustainability! The integral approach. This volume.
- Nei, M. and D. Graur. 1984. Extent of protein polymorphism and the neutral mutation theory. *Evol. Biol.* 17: 73–118.
- Patterson, B. D. and W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos, pp. 65–82. In: L. R. Heaney and B. D. Patterson (eds) *Island Biogeography of Mammals*. Academic Press, New York.
- Pianka, E. R. 1970. On r and K selection. *Amer. Nat.* 104: 592–597.
- Pimm, S. L., H. L. Hones and J. M. Diamond. 1988. On the risk of extinction. *Amer. Nat.* 132: 757–785.
- Pimm, S. L., J. L. Gittleman, G. F. McCracken and M. Gilpin. 1989. Plausible alternatives to bottlenecks to explain reduced genetic diversity. *Trends Ecol. Evol.* 4: 176–177.
- Ralls, K. and J. Ballou. 1983. Extinction: lessons from zoos, pp. 164–184. In: C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde and W. L. Thomas (eds) *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Benjamin/Cummings, Menlo Park, CA.
- Ralls, K. and J. Ballou. 1986. Genetic management of captive populations. *Zoo Biol.* 5: 127–138.
- Ralls, K., J. D. Ballou and A. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conserv. Biol.* 2: 185–193.
- Richter-Dyn, N. and N. S. Goel. 1972. On the extinction of a colonizing species. *Theor. Pop. Biol.* 3: 406–433.
- Robinson, J. G. and K. H. Redford. 1986. Intrinsic rate of natural increase in Neotropical forest mammals: relationship to phylogeny and diet. *Oecologia* 68: 516–520.
- Salwasser, H. 1991. In search of an ecosystem approach to endangered species conservation, pp. 247–265. In: K. A. Kohm (ed) *Balancing on the Brink of Extinction: The Endangered Species Act and Lessons for the Future*. Island Press, Washington, DC.
- Schonewald-Cox, C. M., S. M. Chambers, B. MacBryde and W. L. Thomas (eds) 1983. *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Benjamin/Cummings, Menlo Park, CA.

- Schwartz, O. A., V. C. Bleich and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biol. Conserv.* 37: 179–190.
- Scott, J. M., B. Csuti, J. D. Jacobi and J. E. Estes. 1987. Species richness: a geographic approach to protecting future biological diversity. *BioScience* 37: 782–788.
- Scott, J. M., B. Csuti, K. Smith, J. E. Estes and S. Caicco. 1991. Gap analysis of species richness and vegetation cover: an integrated biodiversity conservation strategy, pp. 282–297. In: K. A. Kohm (ed) *Balancing on the Brink of Extinction: The Endangered Species Act and Lessons for the Future*. Island Press, Washington, DC.
- Seal, U. S. 1978. The Noah's Ark problem: multigeneration management of wild species in captivity, pp. 303–319. In: S. A. Temple (ed) *Endangered Birds: Management Techniques for Preserving Threatened Species*. University of Wisconsin, Madison, WI.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31: 131–134.
- Simberloff, D. 1987. The spotted owl fracas: mixing academic, applied, and political ecology. *Ecology* 68: 766–772.
- Soulé, M. E. 1980. Thresholds for survival: criteria for maintenance of fitness and evolutionary potential, pp. 151–170. In: M. E. Soulé and B. A. Wilcox (eds) *Conservation Biology: An Evolutionary – Ecological Perspective*. Sinauer, Sunderland, MA.
- Soulé, M. E. (ed) 1987. *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Soulé, M. E. 1990. The onslaught of alien species, and other challenges in the coming decades. *Conserv. Biol.* 4: 233–240.
- Soulé, M. E. and B. M. Wilcox (eds) 1980. *Conservation Biology: An Evolutionary – Ecological Perspective*. Sinauer, Sunderland, MA.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Mgmt.* 47: 893–901.
- Wilkes, H. G. 1983. Current status of crop plant germplasm. *CRC Crit. Rev. Plant Sci.* 1: 133–181.
- Williams, J. T. 1988. Identifying and protecting the origins of our food plants, pp. 240–247. In: E. O. Wilson (ed) *Biodiversity*. National Academy Press, Washington, DC.
- Wilson, E. O. 1988. The current state of biological diversity, pp. 3–18. In: E. O. Wilson (ed) *Biodiversity*. National Academy Press, Washington, DC.