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Managing Genetic Diversity in Captive Breeding and Reintroduction Programs

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Introduction

Captive breeding and reintroduction are the most intensive (and hence most expensive) forms of wildlife management (Conway 1986, Kleiman 1989). The need for such intensive management is usually a sign that society has failed to adequately restrict some human impact on a taxon, such as habitat loss and degradation, direct or indirect mortality, or the introduction of an exotic species. Thus, a captive breeding and reintroduction program for a taxon of conservation concern should be part of a comprehensive conservation strategy that also addresses the problems affecting the taxon in the wild (Ballou in press, Foose 1989, Povilitis 1990). Under these circumstances, such programs can make substantial contributions to the preservation of endangered taxa. For example, captive breeding and reintroduction has enabled the peregrine falcon (*Falco peregrinus*) to repopulate much of North America (Cade 1990) and Arabian oryx (*Oryx leucoryx*) have been successfully reintroduced in several areas of their original range (Stanley-Price 1989).

Once the need for a captive breeding program is identified, it is advisable to initiate the program as soon as possible. Starting the program before the wild population has been reduced to a mere handful of individuals increases its chances of success. This strategy provides time to solve husbandry problems, increases the likelihood that enough wild individuals can be removed to give the new captive population a secure genetic and demographic foundation, and minimizes adverse effects of removing individuals on the wild population.

Over the last decade, it has generally become recognized that captive populations of threatened and endangered species should be managed to maintain the genetic diversity present in the wild individuals from which the captive population is descended (Hedrick and Miller 1992, Hedrick et al. 1986, Ralls and Ballou 1986, Soulé et al. 1986, Templeton 1990). The first formal cooperative breeding programs designed to maintain genetic diversity in captive populations were the Species Survival Plans of the American Association of Zoological Parks and Aquariums (AAZPA) (Foose and Seal 1986); similar programs now have been developed in several other countries (Hutchins and Wiese 1991) and efforts at international coordination are underway (Jones 1990).

Managing captive populations to maintain maximum genetic diversity counters unwanted genetic changes in captivity due to selection (Frankham et al. 1986) and avoids possible deleterious effects of inbreeding (Ralls et al. 1988). It also preserves future options for both the taxon and its managers (Templeton 1990): without genetic variation, the captive individuals or their reintroduced progeny would be unable to adapt to future environmental changes (Frankel and Soulé 1981) and various management strategies, such as within-family selection against recessive lethals or serious pathologies (Foose et al. 1986), would not be possible options.

Here, we summarize current management techniques for maintaining genetic diversity in captive populations and the genetic and demographic aspects of selecting captive individuals for reintroduction to the wild. We illustrate the use of these techniques with data from captive breeding and reintroduction programs for two avian species, the Guam rail (*Rallus owstoni*) and California condor (*Gymnogyps californianus*), and two mammalian species, the black-footed ferret (*Mustela nigripes*) and golden lion tamarin (*Leontopithecus rosalia*).

A few of the last rails were captured for a captive breeding program before the remaining rails, and most of the birds on Guam, were exterminated by the introduced brown tree snake (*Boiga irregularis*) (Witteman et al. 1990). The condor population was extremely small and rapidly declining when the last wild individuals were brought into captivity (Dennis et al. 1991, Wallace in press). A distemper epidemic reduced the only known wild ferret population to a few individuals that were used to begin the captive breeding program (Thorne and Belitsky 1989). The tamarin population was in danger of extinction due to the destruction of most of its Atlantic forest habitat in Brazil and illegal capture for pet trade (Kleiman et al. 1986).

The rail project is a joint program of the U.S. Fish and Wildlife Service (USFWS) and the AAZPA's SSP; the condor program is directed by the USFWS with the advice of the Condor Recovery Team (Wallace in press); the ferret program is overseen by the Wyoming Game and Fish Department, the USFWS and the AAZPA's SSP; and the tamarin program is coordinated by the Golden Lion Tamarin International Cooperative Research and Management Committee (Kleiman et al. 1986).

What Do We Mean by Genetic Diversity?

The genetic variation present in individuals, populations or species can be measured and compared in several ways (Hedrick et al. 1986, Lande and Barrowclough 1987). One common measure is the amount of heterozygosity. Most vertebrate individuals are diploid, that is, each has two alleles at every genetic locus. An individual inherits one of these alleles from its mother, via an egg, and the other from its father, via a sperm. Thus, a typical vertebrate individual is either homozygous (the two alleles are the same) or heterozygous (the two alleles are not the same) at each of its approximately 100,000 genetic loci (Gilpin and Wills 1991). The concept of heterozygosity is illustrated in Table 1 with hypothetical data on the genotypes of 10 individuals at three genetic loci. At locus A, all 10 individuals are homozygous for the dominant allele A. At locus B, individuals 1, 3, 6, 7 and 9 are homozygous for the dominant allele B, individual 10 is homozygous for the recessive allele b, and individuals 2, 4, 5 and 8 are heterozygous with one B allele and one b allele. At locus C, only individual 2 is homozygous. The heterozygosity of an individual can be estimated as the average heterozygosity across the number of loci for which we have data (Hedrick et al. 1986). From our example, individual 4 has the highest heterozygosity (2 of 3 loci are heterozygous = 0.67). The heterozygosity of a population (H bar) is the individual heterozygosities averaged over all the individuals within the population (Table 1: H bar = 0.43; Hedrick et al. 1986). Typically in mammals, population heterozygosity is about 4 percent (Nevo 1978).

Table 1. Hypothetical data on the genotypes of 10 individuals at three genetic loci: A, B and C. Dominant alleles are represented by capital letters and recessive alleles by lowercase letters. Locus C has a dominant allele, C, and four recessive alleles, c_1, c_2, c_3 and c_4.

Individual number	Genotype at Locus A	Locus B	Locus C
1	AA	BB	Cc_1
2	AA	Bb	c_1c_1
3	AA	BB	Cc_2
4	AA	Bb	Cc_3
5	AA	Bb	c_1c_2
6	AA	BB	c_1c_3
7	AA	BB	Cc_4
8	AA	Bb	c_1c_4
9	AA	BB	c_1c_3
10	AA	bb	c_1c_2

Another aspect of genetic variation is allelic diversity or the number of different types of alleles at a locus. Empirical studies have shown that there is little or no variation at many loci, that is, most or all individuals in the population are homozygous for a single allele (as at locus A in our example) (Fuerst and Maruyama 1986). If other alleles occur at the locus, they are very rare. Other loci are highly polymorphic, that is, several alleles at the locus are reasonably common within the population. The concept of allelic diversity also is shown in Table 1. There is no allelic diversity at locus A, as only one allele, A, is present. There is some allelic diversity at locus B, with two alleles, B and b present. There is a great deal of allelic diversity at locus C, where there are five alleles present: the dominant allele C and four recessive alleles represented as c_1, c_2, c_3 and c_4.

Although the data shown in Table 1 are hypothetical, actual data of this type, at least for some small fraction of the many genetic loci present in any species, can be obtained for most wild populations by collecting blood or tissue samples and using various descriptive genetic techniques, such as protein electrophoresis (Lewontin 1974).

Pedigrees Versus Laboratory Data

The goal of current strategies for maintaining genetic diversity in a captive population is to preserve as much as possible of the genetic variation, in the form of heterozygosity and allelic diversity, that was present in the wild individuals used to found the population. Laboratory data on the extent of genetic variation present in the population are not required; we can manage to preserve genetic variation with no knowledge of how much genetic variation there is to preserve!

Current techniques rely on models of the expected loss of heterozygosity predicted by population genetic theory in the absence of mutations and selection (Frankel and Soulé 1981, Lacy et al. in preparation, Soulé et al. 1986) and various analyses of the captive population's pedigree, including computer simulations of the loss of hypothetical alleles (Ballou in press, Hedrick and Miller 1992, Lacy 1990, MacCluer et al. 1986). Thus, although laboratory measures of genetic variation are not required, accurate pedigree data are essential. The captive individuals must be housed in such a way that the parentage of all offspring is known with certainty and detailed records on all individuals born in captivity, including their sire, dam, birth date and death date, must be maintained (Glatston 1986). A number of computer software systems have been developed for this purpose (ISIS 1991, Odum 1990).

Even when descriptive genetic data of the type shown in Table 1 do exist for a specific captive population, as for example, the rail (Haig et al. 1990), management to maintain genetic variation is still based on the population's pedigree rather than the actual alleles known to be present at a few loci in each individual. The reason is that heterozygosity measured by electrophoresis is a poor estimator of the overall level of genetic diversity of the individual (Hedrick et al. 1986). Managing to preserve diversity in a small part of an individual's genome based on descriptive genetic data (such as the results of electrophoretic surveys) results in greater over-all loss of diversity than managing on the basis of pedigree analyses (Haig et al. 1990, Hedrick et al. 1986, Lande and Barrowclough 1987). Thus, management to preserve genetic diversity revealed by electrophoresis is generally not advisable.

A specific form of management based on descriptive genetic data rather than pedigree analysis was advocated by Hughes (1991). He recommended management to maintain allelic diversity (as indicated by the use of DNA probes and antibody reagents) at the major histocompatibility complex (MHC), because the MHC is known to play an important role in pathogen recognition (Klein 1986, Miller and Hedrick 1991). However, this approach has not been adopted by those responsible for the management of captive populations. The arguments against it, including the fact that it would result in greater over-all loss of genetic variation than management based on pedigrees, have been presented by Gilpin and Wills (1991), Miller and Hedrick (1991), and Vrijenhoek and Leberg (1991).

Phases of a Captive Breeding Program

Ideally, the first step in the development of a captive breeding program is consensus among all concerned parties (agency personnel, outside scientific advisors, non-governmental conservation groups) that such a program likely would benefit a specific taxon. This step may be difficult to achieve as value systems differ and there are no precise scientific guidelines for the optimal point at which to begin capturing animals for a captive breeding program. However, the IUCN Policy Statement on Captive Breeding recommends starting a captive population well before the wild population reaches a critical state: "Management to best reduce the risk of extinction requires the establishment of captive populations much earlier, preferably when the wild population is still in the thousands. Vertebrate taxa with a current census below one thousand individuals in the wild population require close and swift cooperation between field conservationists and captive breeding specialists to make their efforts complementary and minimize the likelihood of extinction. . . ." (IUCN 1987). This recommendation does not imply that a full-fledged captive breeding and reintroduction program is needed for all wild taxa with populations in the thousands but rather than it often is prudent to develop and maintain the capacity to implement such a program (captive animals, proven husbandry and reintroduction techniques) as a safety measure. Although probably not appropriate for all taxa, the "below one thousand individuals in the wild" criterion from this IUCN statement is being tried as a "general benchmark," indicating that a captive breeding program may be advisable (Foose 1991, Seal 1991).

Once a captive breeding program is initiated, its subsequent development can be pictured as three phases: the founding phase, during which the population is initiated; the growth phase, during which the population rapidly increases to the final size desired by its managers (the "target" population size); and the carrying capacity phase, during which the population is maintained at its target size (Figure 1) (Ballou in press). Management concerns change as the population progresses through these phases. The major concerns during each phase are discussed in turn below.

Management Concerns During the Founding Phase

Initially, management concerns center upon removing individuals with minimal impact on the wild population, getting the species to breed reliably in captivity, setting general goals and plans for the captive population, and obtaining enough wild individuals to ensure a sound genetic and demographic base for the captive population.

Removing animals from the wild. Ways of reducing the impact of removing the captured animals from the wild population include removing eggs from nests (many birds, e.g., condors, will lay another egg to replace the one removed); capturing dispersing young, which often have a high mortality in the wild, e.g., ferrets; and

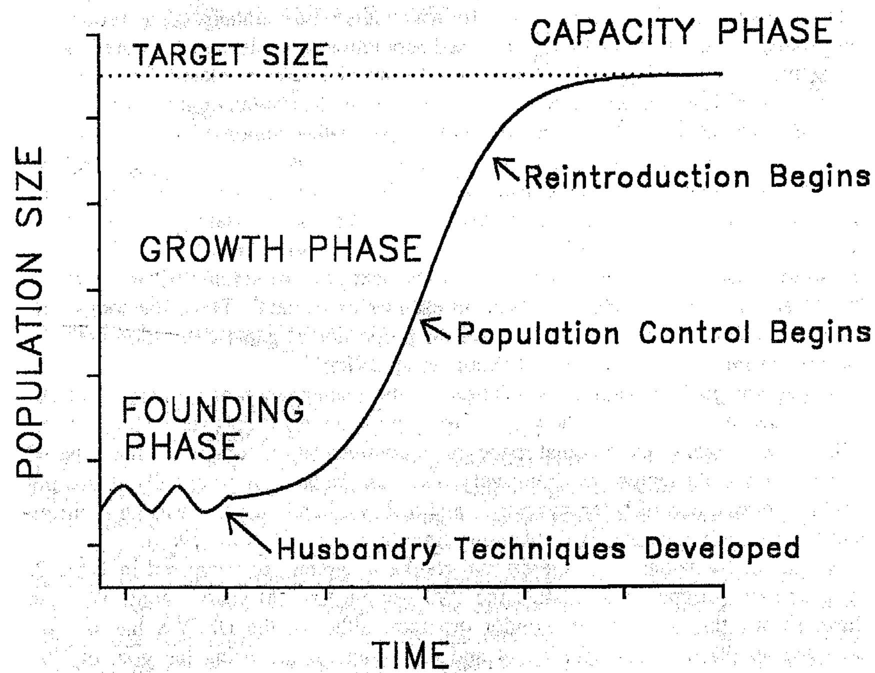

Figure 1. The development of a generalized captive breeding and reintroduction program from the founding to the capacity phase. The captive population usually is subdivided at some point in the growth phase.

using young animals which have become separated from their mothers, e.g., California sea otter (*Enhydra lutris*) pups sometimes wash ashore.

If the program is begun before the wild population has reached the "crisis" stage, it is wise to begin with the capture of a few wild individuals (or the capture of some wild individuals belonging to a closely related "model" taxon) to enable the development of suitable husbandry techniques. There are many taxa, for example, kangaroo rats (*Dipodomys*), that zoos do not know how to breed reliably in captivity. In such cases, research on genetics, behavior, nutrition, disease or reproduction may be necessary to find the reasons for the lack of breeding success, and research takes time. In the case of the tamarin, the husbandry problems concerned both behavior and nutrition (Kleiman et al. 1986). Once they were solved, in the mid-1970s, the captive population grew rapidly (Figure 2). Initial problems in maintaining and breeding the ferret population involved disease and reproductive synchronization of the males and females during the short breeding season; they were overcome by 1989 (Thorne and Oakleaf 1991). Siberian polecats (*Mustela putorius*) and domestic ferrets (*Mustela putorius furo*) were used as surrogates for ferrets during the breeding season and for research on reproductive biology (Wildt et al. 1989). Both rails and condors bred fairly well in captivity from the start, because zoos had experience with these or closely related species (Derrickson 1987, Wallace in press).

General goals and overall planning. Genetic goals for captive populations are specified in terms of the proportion of genetic variation (expressed as heterozygosity) to be maintained and the length of time for which it is to be maintained. The proportion of genetic variation retained within a closed population depends upon the population's effective size and the number of generations for which it remains closed. The effective size of a population can be defined as the size of an ideal population (a hypothetical population with specific properties central to population genetics theory—*see* Falconer 1981, Hedrick 1985) that would have the same rate of loss of heterozygosity as the actual population under consideration. The effective population size generally is only a fraction of the actual population size (Lande and Barrowclough 1987). Generation length is critical because some genetic variation is lost when the parent generation passes its genetic variation on to the next generation (an offspring contains only half the genetic material present in each of its parents). Thus, the longer the generation time of a species, the smaller the proportion of genetic variation that will be lost during a given time period (Soulé et al. 1986).

A general goal for captive populations is the maintenance of 90 percent of the genetic variation present in the source (wild) population for 200 years (Soulé et al. 1986). The panel of experts that made this recommendation concluded that "the 90 percent threshold represents, intuitively, the zone between a potentially damaging and a tolerable loss of heterozygosity" and that two hundred years was an arbitrary but "reasonably conservative" planning time-frame (Soulé et al. 1986).

Goals for the tamarin, rail, ferret and condor programs are compared in Table 2. The tamarin program has adopted the "90 percent for 200 years" goal. We also have shown this goal for the condor program, although the USFWS has not yet adopted an official goal. The ferret and rail programs are using the goal of "90 percent for 50 years." Planning for a shorter time period was deemed appropriate in these cases due to the short generation times for these species (*see* Table 2) and plans for the rapid re-establishment of several wild populations (Ballou and Oakleaf

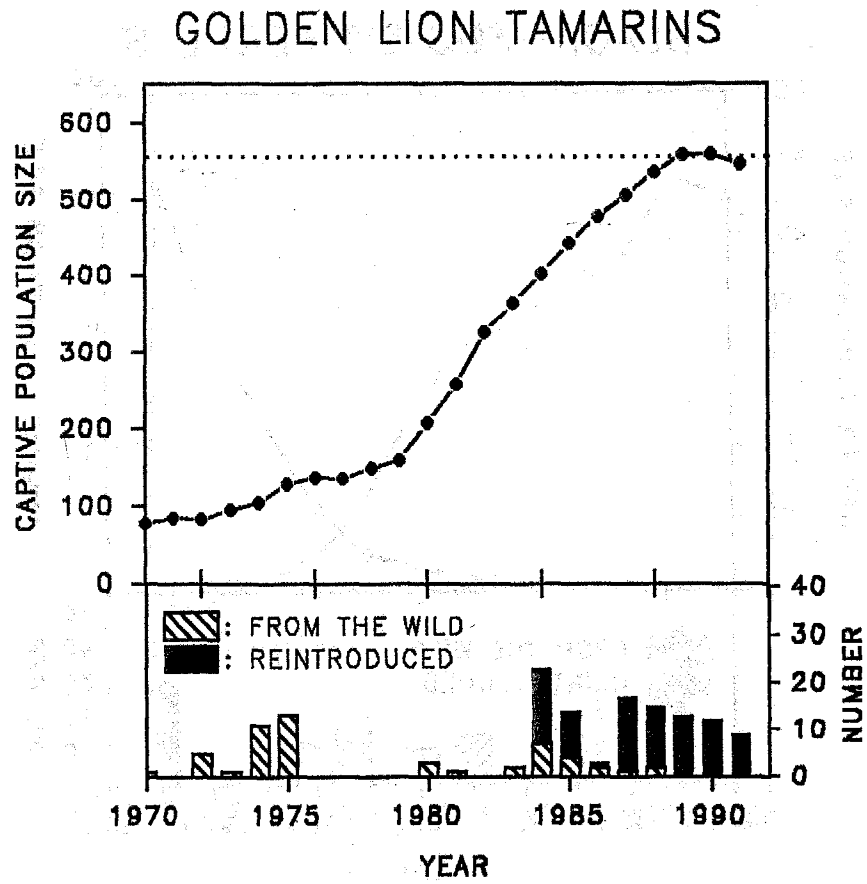

Figure 2. The historical development of four captive breeding and reintroduction programs: A) golden lion tamarins; B) Guam rails; C) black-footed ferrets; D) California condors. The dotted line indicates the target size for each captive population.

1989, Derrickson 1991). Some programs may adopt the "90 percent for 200 years" goal initially and change to a less demanding one, e.g., "90 percent for 100 years" if the size and viability of the wild population(s) improve to the point where the captive population is less critical for preserving the genetic variation of the species. This approach has been considered by the tamarin management committee.

Setting a specific goal enables estimates, based on population genetics theory, of the number of wild animals that must be captured and induced to breed in captivity (the number of "founders" needed for the captive population) and the target population size (the number of individuals that must be maintained in captivity during the planning period) needed to meet the goal (Soulé et al. 1986). Planning to retain a higher percentage of genetic variation increases the necessary target size. For example, maintaining 92 percent, instead of 90 percent, of the ferret genetic variation for 50 years would require a target population of 2,700 rather than 500 individuals.

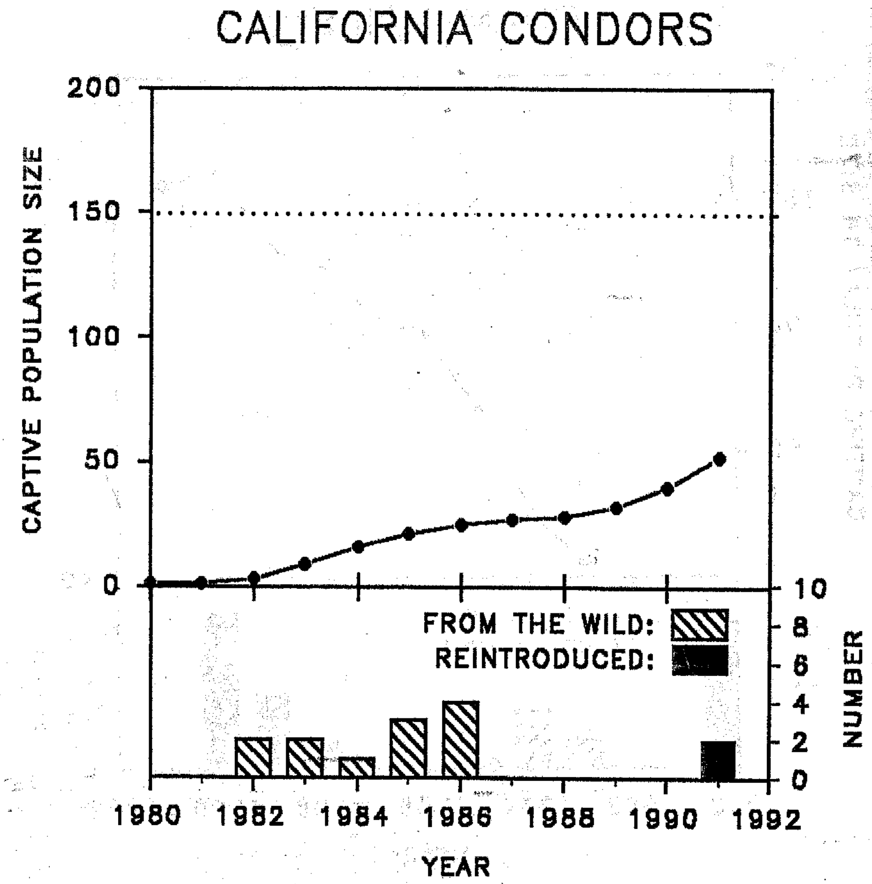

Figure 2D. continued

be a compromise between the number of animals required according to genetic and demographic considerations and the limited resources available (Ballou and Foose in press).

The target population size determines the number of breeding animals in the captive population and, thus, the potential number of offspring available for reintroduction each year. Thus, it could conceivably be desirable to specify a target size above the number of individuals required for genetic reasons if very large numbers of young were wanted for reintroduction.

Acquiring the remaining founders. Once the taxon is breeding well in captivity, it is desirable to capture the required number of founders as soon as possible. The speed with which this can be accomplished depends upon many variables, such as the available captive facilities and the impact of removing individuals from the wild population. The founders for the ferret, rail and condor populations were obtained within a three to five year period (Figure 2, B–D). The original founder animals (or

Table 2. The goals and founder status of four captive breeding programs with reintroduction components. Species listed in order of increasing number of generations encompassed in the program length.

	Species			
	California condor[a]	Black-footed ferret	Guam rail	Golden lion tamarin
Heterozygosity goal	90 percent	90 percent	90 percent	90 percent
Length of program (years)	200	50	50	200
Number of generations	10	20	22	33
Target population size	150	500	150	550
Number wild-caught	14	18	21	69[d]
Number of contributing founders[b]	13	10	13	45
Founder genome equivalents[c]	8	5	5	12

[a]Heterozygosity goal, program length and target population size have not been officially adopted by program managers; other data from Kieler (1991).
[b]Founders with currently living descendants.
[c]The number of theoretically ideal founders taking into consideration loss of genetic diversity in the current captive population (Lacy 1989).
[d]Includes the number of wild-caught tamarins acquired after the captive program was initiated in 1981 in addition to the number of founders and wild-caught individuals alive at the initiation of the program.

their descendants) were already in captivity when the tamarin program was initiated in 1981 (Figure 2, A). However, wild animals continue to be available; the 24 wild tamarins that have been added to the captive population since its initiation were animals turned over to the captive breeding program by authorities that had confiscated tamarins illegally captured from wild populations. In addition, interactive management of the captive and wild tamarin population should expand the founder base for the captive population in the future.

Capturing all the individuals at one location may not obtain an adequate sample of the taxon's genetic diversity (Templeton 1990). Genetic surveys of the wild population(s) using electrophoretic or molecular techniques may be helpful in determining the geographic distribution of genetic variation in the wild and devising the best sampling plan.

Unfortunately, the number of wild animals captured usually does not translate directly into the number of founders. Wild-caught animals may be related, fail to breed or, if they do breed, their descendants may fail to reproduce. For example, although 25 wild ferrets were captured from Meeteetsee, Wyoming, the first 6 died of distemper (Thorne and Belitsky 1989). Several others were known to be parents and offspring, thus reducing the number of potential founders to only 10 presumably unrelated individuals (Ballou and Oakleaf 1989). Furthermore, some potential ferret founders failed to reproduce, while those that did have reproduced unequally, severely skewing their genetic contribution to the population's gene pool. Such processes further erode the genetic contribution of the founders (Lacy 1989). As a result, the current ferret population is founded by the theoretical equivalent (founder genome

(Wildt 1989). Cryopreservation of gametes or embryos can potentially save genetic material from founders or other genetically important individuals, particularly those that fail to breed naturally. Artificial insemination and *in vitro* fertilization can enable genetically desirable matings that would otherwise be impossible due to geographical separation of potential mates or behavioral problems. Embryo transfer to females of a closely related species could be used to increase reproductive rates (Ballou and Cooper in press).

Reproductive rates of captive avian populations often can be increased by the removal and artificial incubation of eggs, as many birds will produce another clutch if their first is removed. This technique has contributed to the rapid growth of both the rail and condor populations. The effect in condors is dramatic: wild condors typically lay one egg every two years but several captive females have produced as many as three eggs per year (Wallace in press).

Coordinating Reintroduction and Captive Breeding Programs

The feasibility and schedule of a reintroduction program can be limited by a variety of factors including habitat availability, funding, the availability of captive-bred individuals for reintroduction and development of species-specific reintroduction techniques. As in the early stages of captive breeding, considerable research, both in captivity and in the field, often is necessary during the early stages of the reintroduction process to develop successful techniques (Stanley Price 1991, Kleiman 1989).

The reintroduction of captive-bred individuals can pose a considerable technical challenge that must be addressed before the reintroduction begins. Trial reintroductions of a closely-related surrogate species may be helpful, e.g., the techniques being used to reintroduce California condors and black-footed ferrets were developed using Andean condors and Siberian polecats (Wallace in press, T. Thorne personal communication: 1991). Behavioral deficiencies are often a problem. Captive-bred ferrets tend to be inefficient at recognizing and avoiding coyotes and other predators; Siberian polecats were used as research surrogates for ferrets for predatory avoidance studies prior to the first ferret reintroduction (Miller et al. 1990). The first tamarins released exhibited poor locomotor and foraging skills. A combination of pre- and post-release training and experience is helping to improve survival rates of reintroduced tamarins (Kleiman et al. 1986).

Reintroductions may be delayed because of insufficient numbers of captive animals if the captive population has not yet completed its growth phase. It generally is advisable to wait until the captive population is near its target size before removing individuals for reintroduction. The advantages of this strategy are that it maximizes both the preservation of genetic diversity in the captive population and the probability that the captive population will not become extinct due to unforeseen chance events.

The first tamarins, rails and ferrets were not reintroduced until the captive populations were at or near the target sizes (Figure 2, A–C). However, some condors are being reintroduced during the growth phase (Table 2, Figure 2, D) due to other pressing concerns, particularly the need to preserve habitat. Reintroducing individuals during the growth phase reduces the growth of the captive population and, thus, increases the number of years required for the population to reach its target size. Although this approach maximizes the number of individuals that are reintroduced in the short-term, the trade-off is that it minimizes the total number that can be reintroduced over the longer term.

Table 3 illustrates these trade-offs based on a simple deterministic model of the condor population under conditions that reflect average reproduction to date (each captive adult female produces about 1.5 chicks/year). The predicted results of two different management plans, A and B are shown. Plan A calls for allowing the captive population to grow to the target size as fast as possible before any chicks are released. Plan B specifies that the captive population be bred at the maximum rate but only be allowed to grow at the minimum rate that will enable it to reach the target size within 10 years (about 11 percent a year). Chicks produced in excess of the number required to achieve this growth rate are used for reintroduction. While this rough model may not be an accurate estimate of the projected growth of the population, it does illustrate that earlier reintroduction (Plan B) results in a smaller number of animals being reintroduced over the 10-year period. Thus, a complex series of trade-offs between the size (and, thus, demographic and genetic security) of the captive population, the advantages of early reintroductions and the advantages of reintroducing more individuals in a given time period must be evaluated when the decision is made to reintroduce individuals during the growth phase.

When the captive population is at its target size, there are two general strategies for producing animals for a reintroduction program. One approach is to pair and breed individuals for the specific purpose of producing excess young for the reintroduction. This is most appropriate when the number of animals to be released and the schedule of reintroduction are predictable relative to the reproductive time-frame

Table 3. Relationships between the growth rate of the captive condor population, the projected length of time until the population reaches its target size (150), and the number of individuals available for reintroduction. Management plan A allows the captive population to grow to 150 as fast as possible before chicks are released, while B reflects a slower rate of population growth due to individuals being removed for reintroduction while the population is in its growth phase; details in text.

	Size of captive population under management plan		Individuals available for reintroduction under management plan	
Year	A	B	A	B
1991	52	52	0	0[b]
1992	69	58	0	9
1993	85	64	0	8
1994	102	72	0	6
1995	120	80	0	6
1996	148	89	0	11
1997	150[a]	101	24	15
1998	150[a]	111	35	20
1999	150[a]	124	42	21
2000	150[a]	135	48	26
2001	150[a]	150[a]	54	28
Total			203	149

[a]Captive population at hypothetical target size.
[b]Two individuals were reintroduced in 1991.

(e.g., inter-birth interval) for that species. This strategy has been followed for the Guam rail. An alternative strategy is to select reintroduction candidates from the existing population and later establish breedings to replace reintroduced individuals. This strategy is useful for programs with relatively unpredictable reintroduction schedules but with high reliability for breeding specific individuals in captivity. For example, the tamarin reintroduction program is primarily limited by funding and habitat availability, not the numbers of animals that can be produced for reintroduction. This results in a less predictable reintroduction schedule. The strategy used in this program has not been to purposefully breed animals for the reintroduction program, but to use animals existing in the population as they are needed and then breed to replace these individuals (using close relatives) in the immediate future. A similar strategy was used in the 1991 ferret and condor reintroductions.

An additional demographic consideration is the effect of removing animals on the age structure of the captive population. Removing young animals for reintroduction is likely to be a common strategy. However, this may have a de-stabilizing effect on the age structure, causing future fluctuations in reproductive rates and population size, particularly if large numbers of young are used (Goodman 1980). Likewise, some types of removal strategies (particularly sex-specific removals) may affect the genetically effective size of the captive population (Ryman et al. 1981). Demographic analyses should be conducted to evaluate the effect of various removal (harvest) strategies on both the demographic and genetic stability of the population.

Although demographic factors, such as the number of offspring that can be produced by a population at its target size, may determine the number of individuals that are potentially available for release each year, genetic methods are important for determining which individuals will be chosen. In the early stages of a reintroduction program, when reintroduction techniques are still being refined and survival of the reintroduced individuals may be poor, the most genetically expendable individuals should be chosen for release. These individuals will have high mean kinship scores and low genome uniqueness scores. An important goal of a reintroduction program, however, is to establish one or more wild populations that contain all the genetic variation present in the captive population. Thus, emphasis will gradually shift to choosing individuals that are not closely related to the individuals already present in a given wild population (Ballou in press). This strategy is currently being followed by the condor, ferret, rail and tamarin reintroduction programs. The tamarin program is slightly more complicated because survival is improved if animals are reintroduced as social groups (families) rather than individuals. Thus, groups of tamarins (a breeding pair and their offspring of various ages), rather than individuals, must be chosen for release.

Summary and Conclusions

(1) A captive breeding program for a taxon of conservation concern should be part of a comprehensive conservation strategy that also addresses the problems affecting the taxon in the wild.

(2) Captive populations for such taxa should be founded well before the wild population has been severely reduced in size. This minimizes the impact of removing individuals from the wild population, assures a solid genetic and demographic base for the captive population, and provides ample time for the captive population to become established prior to the possible need for a reintroduction program.

(3) Captive breeding programs can make their most effective contribution to the conservation of endangered taxa if captive populations are demographically and genetically managed.

(4) Genetic management focuses on maintaining genetic diversity in order to minimize undesirable genetic changes due to selection in the captive environment, avoid the possible effects of inbreeding depression and maintain future options for genetic management.

(5) The number of animals available for reintroduction from a captive breeding program depends on the size and status of the captive population. Numbers can be limited by both genetic and demographic concerns.

(6) Captive breeding and reintroduction programs involve both research and management actions. Although genetic and demographic management techniques for captive populations are fairly well developed and can be applied to most taxa, husbandry and reintroduction techniques tend to be taxon-specific, and existing information often is insufficient to guide the development of a new program. Thus, considerable research and funding are often necessary to develop a successful captive breeding and reintroduction program for a particular taxon.

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Landscape Considerations for Viable Populations and Biological Diversity

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Introduction

Wildlife management typically focuses on individual species. Attention to single species comes historically from management of game species based on maximum sustainable yield concepts (Holt and Talbot 1978). Species need to be examined individually and in different regions of their geographic range to understand habitat requirements (Noon et al. 1980, James et al. 1984, Knopf et al. 1990), but they also need to be considered in the context of other species with which they may coexist. Management for one species may affect other potentially-coexisting species, plus effects of management on other coexisting species that are competitors, predators or parasites may affect demography of target species. In addition, land use practices surrounding a given habitat also may affect the numbers and types of coexisting species as well as population viability, and has generated increased interest in "landscapes." Thus, effects of management practices on biological diversity and population viability need to be considered at several spatial scales.

Landscape refers to interspersion of heterogeneous land forms, vegetation types and land uses (Urban et al. 1987). Increased landscape diversity (greater interspersion and numbers of landscape elements) can increase the numbers of species coexisting in the landscape (Johnston 1947, Johnston and Odum 1956, Crawford et al. 1981). In addition, interspersion of vegetation or "cover" types is also associated with increased population sizes of some species. For example, population sizes of Bobwhite Quail (*Colinus virginanus*) are correlated with indices of cover interspersion (Baxter and Wolfe 1972). Nevertheless, while increased landscape diversity may result in increased plant and animal diversity locally, it may have detrimental effects on habitat suitability for individual species (defined by fitness within the habitats—Fretwell 1972, van Horne 1983) and affect regional diversity. These and other conflicts must be carefully considered when addressing biological diversity in management recommendations. Moreover, many relationships and patterns considered in landscape and fragmentation issues are based on assumptions that are not well-studied. Unproven assumptions must be recognized so that caution can be exercised when generalizing predicted relationships and patterns. Here, I briefly discuss some of these conflicts and assumptions. I do not directly discuss corridor effects because they represent edge habitats and, thus, simply fit in the larger issue of edge effects. I draw largely on avian examples because of my greater familiarity with that literature and because the ideas are general enough to apply to a wider range of taxa.