Limitations of Captive Breeding in Endangered Species Recovery

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Abstract: *The use of captive breeding in species recovery has grown enormously in recent years, but without a concurrent growth in appreciation of its limitations. Problems with (1) establishing self-sufficient captive populations, (2) poor success in reintroductions, (3) high costs, (4) domestication, (5) preemption of other recovery techniques, (6) disease outbreaks, and (7) maintaining administrative continuity have all been significant. The technique has often been invoked prematurely and should not normally be employed before a careful field evaluation of costs and benefits of all conservation alternatives has been accomplished and a determination made that captive breeding is essential for species survival. Merely demonstrating that a species' population is declining or has fallen below what may be a minimum viable size does not constitute enough analysis to justify captive breeding as a recovery measure. Captive breeding should be viewed as a last resort in species recovery and not a prophylactic or long-term solution because of the inexorable genetic and phenotypic changes that occur in captive environments. Captive breeding can play a crucial role in recovery of some species for which effective alternatives are unavailable in the short term. However, it should not displace habitat and ecosystem protection nor should it be invoked in the absence of comprehensive efforts to maintain or restore populations in wild habitats. Zoological institutions with captive breeding programs should operate under carefully defined conditions of disease prevention and genetic/behavioral management. More important, these institutions should help preserve biodiversity through their capacities for public education, professional training, research, and support of in situ conservation efforts.*

Las limitaciones de la cría en cautiverio en la recuperación de especies en peligro de extinción

Resumen: *El uso de la cría en cautiverio para la recuperación de especies ha crecido enormemente en a ños recientes, pero sin un crecimiento concurrente en el reconocimiento de sus limitaciones. Los problemas con (1) el establecimiento de poblaciones cautivas autosuficientes, (2) el escazo éxito en la reintroducción, (3) los altos costos, (4) la domesticación, (5) la exclusión de otras técnicas de recuperación, (6) los brotes de enfermedades, y (7) el mentenimiento de la continuidad administrativa han sido todos signifivativos. Esta técnica ha sido frucuentemente invocada en forma prematura y no debería ser usada normalmente sin antes llevar a cabo una cuidadosa evaluación a campo de los costos y beneficios de todas las alternativas de conservación y de determinar si la cría en cautiverio es esencial para la supervivencia de la especie. Demostrar sim-*

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plemente que una población de una especie esta declinando o ba caído por debajo de lo que sería del tama ño viable mínimo, no constitutye un análisis suficiente como para justificar la cría en cautiverio como medida de recuperación. Debido a los cambios genéticos y fenotípicos inexorables que se producen en ambientes de cautiverio, la cría en cautiverio debería ser una medida última instancia en la recuperación y no una profiláxis o solución a largo plazo. La cría en cautiverio puede jugar un papel crucial en la recuperación de algunas especies, para las cuales no se encuentran a disposición alternativas efectivas en el corto plazo. Sin embargo, esta no debe desplazar a la protección del hábitat y del ecosistema, así como tampoco debe ser invocada en ausencia de esfuerzos comprensivos para mantener o reestablecer poblaciones en hábitats naturales. Las instituciones zoológicas con programas de cría en cautiverio, deberían operar bajo condiciones cuidadosamente definidas en cuanto a la prevención de enfermedades y manejo genético/etológico. Aún mas importante, estas instituciones deben ayudar a la preservación de la biodiversidad a través de su capacidad para la educación pública, el entrenamiento profesional, la investigación, y el apoyo a la conservación in situ.

Introduction

In recent years there has been a tremendous increase in the use of captive breeding for recovering endangered species. Captive breeding techniques have been improving continuously, as have techniques for reintroducing captive-bred animals into the wild. For some species, such as the California Condor (*Gymnogyps californianus*), the Mauritius Kestrel (*Falco punctatus*), the black-footed ferret (*Mustela nigripes*), and the Guam Rail (*Rallus owstoni*), captive breeding has clearly represented the difference between survival and extinction in the short term (Snyder & Snyder 1989; Derrickson & Snyder 1992; Jones et al. 1995; Miller et al., in press).

Despite the important role that captive breeding has had in the recovery of some species, we are concerned that it is being promoted as a recovery technique for many species that may not benefit from it. We note in particular that the World Conservation Union's (IUCN) Captive Breeding Specialist Group, renamed the Conservation Breeding Specialist Group (CBSG), has recently generated a series of Conservation Assessment and Management Plans (CAMPs) that call for long-term captive breeding of numerous taxa. For example, the draft CAMP document for parrots (Seal et al. 1992) recommended long-term captive breeding for roughly half of the 330 parrot species in the world. For vertebrates in general, Seal et al. (1993) recommended captive management for a staggering 1192 (34%) of the 3550 taxa examined. Furthermore, captive breeding is recommended in a remarkable 64% of the 314 approved recovery plans for U.S. endangered and threatened wildlife (Tear et al. 1993). Of special concern are a number of "ark" paradigm proposals that envision long-term preservation of numerous species through captive breeding, followed, perhaps centuries from now, by reintroductions to the wild (Soulé et al. 1986; Foose et al. 1992; Tudge 1992).

Because the implications of such large-scale reliance on captive breeding are profound and because some proposals currently before Congress would revise the Endangered Species Act to greatly emphasize captive breeding, we believe a review of the overall advisability of this technique in species recovery is appropriate. We examine the role of captive breeding in the recovery of endangered animal species, focusing on seven often overlooked limitations of the technique. Although we do not consider plants, we believe our discussion also has relevance to plant conservation (cf. Ashton 1988; Allen 1994; Hamilton 1994). Captive breeding for recovery purposes (i.e., for ultimate reintroductions to the wild) should not be confused with captive breeding for other purposes, such as exhibit, conservation education, or research. Although these latter captive breeding programs may also have conservation value, they have quite different characteristics and entail different precautions.

Our primary conclusion is that captive breeding has a legitimate role to play in the recovery of only a limited number of endangered species and should be employed only when other viable alternatives are unavailable. When it is employed, it should always be tightly coupled with recovery objectives for wild populations and should not be proposed as a long-term solution.

Limitations of Captive Breeding

Achieving Self-sustaining Captive Populations

It is often assumed that self-sustaining captive populations can be readily established for most endangered and threatened taxa. However, only a small percentage of vertebrate or invertebrate taxa have bred in captivity (Conway 1986; Rahbek 1993), and obtaining consistent reproduction and survivorship under captive conditions has proven difficult with many species (Table 1). Failures to breed well in confinement can be traced to a variety of causes, including the lack of psychological, physiological, or environmental requirements (Millam et al. 1988; Merola 1994), inadequate diet (Setchell et al. 1987), effects of hand-rearing (Myers et al. 1988), behav-

Table 1. Examples of endangered species breeding programs that have encountered significant problems in achieving self-sustaining captive populations.

Species	*Problems*	*Reference(s)*
Whooping Crane (*Grus americana*)	low numbers, high mortality, infertility, incompatibility	Lewis (1990)
Kakapo (*Strigops habroptilus*)	low numbers, poor survival	Merton and Empson (1989)
Puerto Rican Parrot (*Amazona vittata*)	low fertility, incompatibility, inbreeding (?)	Snyder et al. (1987), Brock and White (1992)
Hawaiian Crow (*Corvus kubaryi*)	low numbers, low fertility, high mortality, incompatibility	NRC (1992)
Aye-Aye (*Daubentonia madagascariensis*)	low offspring survival	Sterling (1993)
Giant panda (*Ailuropoda melanoleuca*)	low numbers, poor neonate survival, incompatibility	Hu and Wei (1990)
Northern white rhino (*Ceratotherium simum cottoni*)	low numbers, low conception rate	Svitalsky et al. (1993)

ioral incompatibility (Yamamoto et al. 1989), and inbreeding depression (Ralls & Ballou 1983; Danielle & Murray 1986). Identifying these factors can be extremely difficult, and for many endangered taxa effective captive management and husbandry regimes are still unknown even after years of experimentation. Because of poor reproduction, self-sustaining captive populations may never be achieved for some endangered species. For others, large numbers of individuals must be held in captivity to attain the production needed to sustain reintroduction efforts.

Reintroduction

In a recent review of 145 reintroduction programs of captive-bred animals, largely vertebrates, Beck et al. (1994) found only 16 cases (11%) of successfully established wild populations (although with some programs still in progress, this rate may rise over time). Captive-bred stocks also fared relatively poorly in the reintroduction programs reviewed earlier by Griffith et al. (1989). These results suggest major difficulties with establishing wild populations from captive-bred stock.

The causes of failure in reintroductions of captive-bred animals vary greatly from case to case and range from a failure to correct the factors originally causing extirpation to significant behavioral deficiencies in released animals, especially with respect to foraging, predator avoidance, and social behavior. Such deficiencies have been documented in a wide variety of captive-bred animals (e.g., Lyles & May 1987; Kleiman 1989; Miller et al. 1990; Wiley et al. 1992; Fleming & Gross 1993; Snyder et al. 1994). These deficiencies seem especially frequent in species that learn most of their behavioral repertoires and in animals that lack opportunities to associate with wild individuals in natural settings during critical learning periods. Reintroduction attempts with captive-bred individuals of species facing appreciable predation threats in the wild often fail. It is noteworthy that a substantial fraction of the successful reintroductions considered by Beck et al. (1994) involved large species, such as the Arabian oryx (*Oryx leucoryx*) and plains bison (*Bison bison*), that were reintroduced in areas without predators.

Logically, behavioral problems seem least likely in reintroductions of species that lack parental care. However, as a caveat to this assertion, releases of captive-raised juvenile sea turtles, to establish new breeding colonies or reestablish extirpated colonies, have been conducted for decades without documented success (National Research Council 1990). In species with extended parental care the behavioral deficiencies of captive-bred stock have sometimes been overcome by conspecific fostering (Snyder et al. 1987; Wiley et al. 1992). Unfortunately, opportunities for conspecific fostering are few or absent for many endangered species. The alternative of cross-fostering young to adults of other species can lead to behavioral problems in species recognition (Harris 1970; Lewis 1990) and is usually best avoided.

It is still early for safe generalizations, but we suggest that in the absence of fostering, the survival of released captive-reared individuals may often be best with species whose behavior is instinctive, species at the top of food chains or species introduced to predator-free or predator-deficient environments. Results to date suggest that for species whose behavioral repertoires are largely learned, it may be difficult to reestablish wild populations if all individuals are drawn into captivity at any point and if releases are limited to captive-bred individuals (Snyder et al. 1994).

Domestication

Many of the problems affecting captive preservation and reintroduction of endangered species are results of genetic and phenotypic changes that occur in captivity. Modern, conservation-oriented breeding programs attempt to ameliorate the genetic effects of inbreeding, drift, and adaptation to the captive environment through the deliberate and careful control of reproduction, population size, and population demography (Foose & Ballou 1988; Allendorf 1993). This is a difficult task, however, given (1) the practical limitations of controlling reproduction; (2) the dynamic nature of evolutionary forces in small populations; (3) the types of genetic variation to be maintained; and (4) the uncertain nature of selection in the captive environment (Lande 1988; Simberloff 1988). We are particularly concerned that the usual strategy to slow down genetic change—equal breeding of founder family lines—is impractical for many species that do not breed readily in captivity, especially those that are reluctant to accept forced pairings and are resistant to manipulative techniques such as artificial insemination. Even in those critically endangered species for which genetic management is relatively feasible, it is not always implemented (Miller et al. in press).

Captive environments differ greatly from wild environments, and evolutionary processes do not stop because species are in cages (Spurway 1955; Kohane & Parsons 1988; Allendorf 1993). Species become progressively more adapted to captivity even when comprehensive genetic management is practiced. Given a number of generations, one can expect to see populations that differ from wild stocks in significant ways, with most, if not all, of these differences having deleterious effects on fitness in the wild (Mason et al. 1967; Fleming & Gross 1993). Upon release such captive stocks may be incapable of producing viable wild populations and/or may exert deleterious genetic pressures on remnant wild populations (Fleming 1994; Philippart 1995).

Selection for traits such as tameness can often be strong in captivity regardless of whether it is intentional or not. And when selection is strong, major changes can occur quickly. For example, in only 20 generations Belyaev (1979) was able to produce almost fully domesticated forms of silver foxes (*Vulpes fulva*), exhibiting typical dog-like characteristics such as two breeding periods per year, drooping ears, erect tails, and behavioral traits such as tail-wagging and a tendency to lick hands and faces of humans (all characteristics that are absent from wild fox populations).

Domestication can be especially rapid in certain fishes and invertebrates (Moyle 1969; Myers & Sabath 1980; Swain & Riddell 1990; Johnsson & Abrahams 1991), possibly due to the high potential fecundity of individuals and short generation times. Many insects, for example, quickly undergo major changes in behavior and morphology under captive conditions. Because of the magnitude of such changes, efforts to reestablish the large copper butterfly (*Lycaena dispar*) in the United Kingdom have focused on use of endangered wild stocks from other countries rather than available captive-bred stocks (Pullin 1993).

Behavioral traits that are learned or culturally transmitted are especially prone to rapid loss in captivity, and genetic management provides no relief from these losses. For many species captive populations may become resistant to reestablishment in the wild for behavioral reasons alone, and within very few, sometimes only single, generations. For example, in species in which young learn long, annual migrations by associating with experienced individuals, the first captive-produced generation may not migrate properly in the absence of a wild population or even in the presence of a wild population if it does not include parental individuals (Akçakaya 1990). Behavioral changes induced by captivity may be the most significant problem when and if we try to unload the "ark" (Lyles & May 1987).

How reversible is domestication? Feral populations of domestic cats (*Felis catus*) have become established from captivity in many regions and with phenotypes reverting to wild appearance relatively quickly. But, feral populations of many domesticated forms are unknown, except in predator-free environments. For example, chickens (*Gallus gallus*) and canaries (*Serius canarius*) have failed to establish wild populations anywhere except on predator-free islands (Derrickson & Snyder 1992). The inability of Wild Turkeys (*Meleagris gallopavo*) to form wild populations after only a few generations in captivity has been thoroughly examined (Leopold 1944; Knoder 1959). In this species domestication effects are apparent in certain features of the endocrine and nervous systems. Size of the adrenal glands rapidly declines in captive flocks and seems closely tied to a loss of the physiological and behavioral traits essential for survival in the wild (Knoder 1959).

We believe the implications of progressive genetic and phenotypic changes are considerably more serious than commonly recognized. Proposals based on the "ark" paradigm are built on a misconception of constancy or near constancy of captive populations through time. For many species long-term captive breeding, despite all efforts to slow changes, may result in domesticated forms with low reestablishment potentials.

Because of progressive domestication, we should abandon any general expectations that we can "preserve" endangered species in captivity without significant change over the long term and limit captive breeding programs to short-term situations where animals will be returned to the wild as soon as possible. Thus, captive breeding programs for reintroduction should not be started any sooner than is clearly necessary, and "prophylactic" captive breeding should be avoided.

Disease

Some evidence exists that endangered species may have enhanced susceptibility to disease because of reduced genetic diversity that can result from small population size (O'Brien & Evermann 1988; Thorne & Williams 1988). Whether or not this is true, disease problems

Table 2. Examples of recent epizootics in captive populations of endangered species.

Species	*Disease*	*Reference(s)*
Whooping Crane (*Grus americana*)	equine encephalitis	Dein et al. (1986)
Red-crowned (*Grus japonensis*) and Hooded (*G. monacha*) Cranes	inclusion body disease	Docherty and Romaine (1983)
Mauritius Kestrel (*Falco punctatus*)	herpes virus, hepatitis	Cooper (1993)
Mauritius Pink Pigeon (*Nesoenas mayeri*)	herpes virus	Snyder et al. (1985)
Puerto Rican Plain Pigeon (*Columba inornata wetmorei*)	coccidiosis, capillaria	Arnizaut and Perez-Rivera (1991)
Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*)	sarcocystis	D. Thomsen, pers. comm.
White-winged Wood Duck (*Carina moschata*)	avian tuberculosis	Cromie et al. (1989)
Bali Mynah (*Leucopsar rothschildi*)	avian pox, atoxoplasmosis	Landolf and Kocan (1976), Partington et al. (1989)
Addax (*Addax nasomaculatus*) and spider monkey (*Ateles geoffroyi frontatus*)	pseudotuberculosis	Welsh et al. (1992)
Black-footed ferret (*Mustela nigripes*)	distemper	Carpenter et al. (1976)
Green sea turtle (Chelonia mydas)	chlamydiosis	Jacobson (1993)
Aruba Island rattlesnake (*Crotalus durissus unicolor*)	ophidian paramyxovirus	Odum and Goode (1994)

have been common in captive populations of endangered species (Table 2).

The frequency of disease outbreaks in captive collections is partly a result of enhanced exposure, especially to exotic pathogens. The prevalence of international wildlife trade and the normally close juxtaposition of diverse species in zoos and private collections have brought many species into contact with diseases and parasites for which they have little resistance (Derrickson & Snyder 1992; Bush et al. 1993; Jacobson 1993). Although disease risks also exist for wild populations, such risks often involve diseases to which the populations have had previous exposure and have developed some resistance. When serious disease problems arise for wild populations (e.g., sylvatic plague and distemper for black-footed ferrets), the diseases involved are often suspected or known to be of exotic origin (Miller et al., in press).

Funding for the study of wildlife diseases has been poor, diagnostic capabilities are not on a par with those for human diseases, and sophisticated tests and vaccines are not available for many pathogens (Worley 1993). Further, standard quarantine periods are too brief for reliable detection of many slow-acting diseases. Some serious diseases can remain latent in asymptomatic carriers for long periods and suddenly manifest themselves when animals come under stress (Partington et al. 1989). Cleansing a facility contaminated with environmentally persistent pathogens can necessitate facility demolition, soil and substrate removal, and euthanasia of potentially infected individuals (Gough 1989).

Because of the existence of slow-acting, yet serious diseases that cannot be detected reliably in carrier individuals (e.g., psittacine proventricular dilation syndrome, avian tuberculosis, paratuberculosis, salmonellosis, Pacheco's disease and other herpes infections), there are always risks that release programs may inadvertently infect wild populations with pathogens to which they lack resistance, even with intensive pre-release screening for diagnosable diseases. These risks are presumably greatest when reintroduction programs use individuals from open, multi-species facilities outside the normal range of the species or when reintroductions use confiscated animals with unknown histories. Although risks also exist for translocations of animals from one wild location to another, the chances of contact with exotic diseases is generally less in such releases than in releases from open, multi-species captive environments as long as transfers are made within historic populations.

Many reestablished populations of Wild Turkeys in the midwestern U.S. are infected with a hematozoan parasite (*Plasmodium kempi*), apparently resulting from translocations of infected birds (Castle & Christensen 1990). Similarly, a virulent upper respiratory mycoplasma disease in wild desert tortoises (*Xerobates agassizii*) and gopher tortoises (*Gopherus polyphemus*) is believed to have resulted from releases of infected captive individuals (Jacobson 1993). Woodford and Rossiter (1994) list many additional cases of inadvertent introductions of diseases into wild populations through releases of contaminated captive-bred or translocated wild-caught animals. Clearly there are appreciable risks to wild populations through releases of captive-bred or translocated wild animals (cf. Snyder et al. 1994), and these risks are often not limited to the species reintroduced (examples in Woodford & Rossiter 1994).

Griffith et al. (1993) reported that animals were not subjected to physical examinations by a professional biologist or veterinarian in 24% of the reintroductions they reviewed. In the survey by Beck et al. (1994) medical screening was practiced in only 46% of the reintroduction programs. Because of the potential significance of disease problems, the CBSG and the American Zoo and Aquarium Association hosted a symposium in 1992 to develop health screening protocols for reintroductions (Wolff & Seal 1993). Unfortunately, because screening methods do not exist for many slow-acting pathogens and because new diseases continue to crop up, the only way to minimize disease risks during reintroductions is to (1) screen intensively for diseases that can be detected and (2) be certain that released stocks have had a long history of non-exposure to potential disease carriers. The latter is effectively impossible in the open, multi-species environments that characterize most public and private zoological collections.

Basic veterinary principles suggest that captive breeding for recovery should be done under the following conditions: (1) captive populations should be maintained in isolated single-species facilities that do not regularly exchange stocks with other facilities; (2) captive breeding should be conducted within the natural range of the species to reduce exposure to exotic pathogens and in at least two geographically separate facilities; (3) founder stock should not be drawn from open, multi-species facilities, but should be taken directly from the wild or from single-species facilities within the natural range that have good histories of disease prevention; and (4) facilities should be closed to the public, and staff should practice rigorous disease-prevention methodology, including strict avoidance of contact with other captive stocks.

These recommendations are based on the position advanced by Ashton and Cooper (1989) that exclusion of pathogens is a much more effective way to avoid problems than attempting to eliminate pathogens once they are established. Thus, strong efforts should be made to prevent exposure of captive stocks to microorganisms and parasites not normally present in their wild populations (we are not, however, advocating maintenance of stocks under completely sterile conditions). Unless such efforts are made, the risks of introducing exotic pathogens into captive and wild populations are substantial.

Most of the precautions we advocate are employed by some captive breeding programs for endangered species (such as California Condor; Puerto Rican Parrot [*Amazona vittata*]), but few are employed by the majority of programs. Unfortunately, comprehensive disease precautions substantially inflate the costs of captive breeding, especially the needs for isolated facilities and separate staffs to care for the animals. Few zoological institutions can afford to practice these precautions and most rely mainly on a quarantine of incoming stock for 30-60 days to reduce the chance of disease outbreaks. Such quarantine can reveal only a fraction of disease-infected animals, and disease outbreaks remain common in open, multi-species institutions (Shima & Osborn 1989).

Our orientation and emphasis on disease risks are a consequence of (1) repeated personal experiences with serious diseases in a variety of captive-breeding and reintroduction programs in which the above precautions were not taken; (2) a virtual absence of such problems in our experience with programs taking many of the above precautions; and (3) a growing realization that the failure of many programs to implement thorough precautions represents a significant risk to wild populations. We are not opposed to all reintroduction efforts from a disease standpoint, and we recognize that disease risks may vary substantially from one taxonomic group to another. Nevertheless, costs of comprehensive disease precautions should be accepted as intrinsic to all captive-breeding efforts for reintroduction. The potentials for future disasters like the chestnut blight, Dutch elm disease, whirling disease of trout, and mycoplasma disease of tortoises should engender an attitude of considerable caution and humility, not one of denial. The recent decision of the U.S. Fish and Wildlife Service to abandon plans to move highly endangered Puerto Rican Parrots to an open, multi-species environment on the mainland (Wilson et al. 1994) is exactly the sort of disease-risk assessment that should become routine throughout the conservation community.

Financial and Physical Resources

The costs of captive breeding programs for recovery of endangered species sometimes run on the order of a half-million dollars per year per species (Derrickson & Snyder 1992). Further, zoological institutions do not have enough space to accommodate viable captive populations for all species that are threatened with extinction (Conway 1986; Soulé et al. 1986; Rahbek 1993)—assuming that captive breeding might be advisable for all these species. If captive breeding for endangered species were to be limited to closed, single-species facilities, as we believe it generally should be, the shortfalls in space and financial resources would be even more daunting.

To counter the space limitations in zoological institutions, Foose and Seal (1992) advocated the concept of nucleus populations. Although these populations (generally under 100 individuals) would be too small to maintain long-term genetic diversity, diversity would be maintained through periodic importations of wild stock. However, Willis and Wiese (1993) showed that the frequency of importations required to maintain genetic diversity in nucleus populations is at least an order of magnitude greater than assumed by Foose and Seal (1992) and is impractical for many species.

Some costs of captive breeding endangered species can be met by institutional revenues. To the extent that institutions limit themselves to showy endangered species, captive breeding can make economic sense. Unfortunately, most endangered species are visually unspectacular, so there is little potential to pay for captive propagation of these species from their own exhibit earnings.

Private breeders are often proposed as an alternative to zoos for breeding endangered species (Clubb 1992), but effective long-term conservation programs are unlikely to come from this sector. Like most zoological institutions, private breeders have been generally unwilling to maintain single-species facilities and separate staffs for endangered species. In addition, genetic management of captive stocks has typically been lax among private, captive breeders, with widespread deficiencies in record-keeping (for example, clouded leopard [*Neofelis nebulosa*], S. Millard, personal communication) and a fascination with hybridization of species and races (such as blue iguana [*Cyclura nubila lewisi*], Burton 1993). Conflicts of interest over ownership of animals and reluctance of individual breeders to cooperate with one another continue to impede programs (Clubb 1992).

In general, the financial resources needed for comprehensive captive breeding of endangered species are not likely to be available either in zoological institutions or among private captive breeders. Both sectors are eager to breed endangered species, but neither can be expected to do it comprehensively without a major infusion of funding from other sources. Unfortunately, financial support from government and private sources is quite limited and usually materializes only for species with substantial public appeal.

In comparison, the monies needed for effective in situ conservation efforts are often much more modest (Leader-Williams 1990; Balmford et al. 1995). Although we recognize that some in situ conservation efforts are costly, the general emphasis on habitat protection inherent in in situ approaches means that multitudes of species beyond particular target species are simultaneously conserved. Consequently, the costs involved should generally be considered those of saving entire ecosystems, rather than those of conserving a single species. From this viewpoint, the true cost differentials between in situ and ex situ approaches may often be much greater than the single order of magnitude calculated for large mammals by Balmford et al. (1995).

Preemption of Other, Better Techniques

Much has been said about difficulties in moving funds between ex situ and in situ approaches (Conway 1995), and in some cases we agree that funds are nontransferable. It is also valid to suggest that in some cases funds for in situ efforts have originated largely as an extension of funding for captive breeding. Nevertheless, in diverse conservation programs, in both public and private sectors, we have frequently dealt with situations of funding competition between these approaches and are acutely aware of how one approach often preempts the other, sometimes to the detriment of crucial in situ needs.

For example, despite requests over a period of years from the California Condor Recovery Team, the U.S. Fish and Wildlife Service has until recently declined to fund a proposal to conduct toxicity studies of alternatives to lead bullets, which could solve the problem of lead poisoning in Condors in the wild (see Wiemeyer et al. 1988; Snyder & Snyder 1989). Meanwhile captive breeding and releases have continued to be funded at more than \$1.0 million annually (including contributions from zoological institutions). Fortunately, the modest funding (~\$30,000) needed for the toxicity studies has now been secured (Anonymous 1994).

For another example, highlighting a black-footed ferret captive breeding and reintroduction program has made it easy for the federal government to deflect attention away from the destruction of ferret habitat through prairie-dog eradication campaigns. In fact, the U.S. Fish and Wildlife Service has determined recently that the captive ferret population is the only "essential" ferret population, in spite of a clear mandate from the Endangered Species Act to recover the species in the wild (Miller et al. in press). Although captive breeding of ferrets, like that of California Condors, is clearly a necessary conservation activity, both species' programs have suffered in recent years from a lack of balance between efforts aimed at captive breeding and reintroduction and those aimed at ameliorating limiting factors in the wild.

Thus, captive breeding can divert attention from the problems causing a species' decline and become a technological fix that merely prolongs rather than rectifies problems (Frazer 1992; Meffe 1992; Philippart 1995). Long-term solutions are often politically more difficult than captive breeding solutions, so it is tempting for managers to deemphasize efforts for wild populations once captive populations are in place.

When captive breeding is tightly coupled with efforts to save wild populations, it can help lead to habitat preservation by serving as a focus for generating public interest in the plight of a species (Durrell & Mallinson 1987; Mallinson 1988). Unfortunately, in practice the connection between captive breeding and habitat preservation is sometimes tenuous. Captive breeding can become an end in itself and may undermine rather than enhance habitat preservation by reducing the urgency with which this goal is pursued. The existence of a captive population can give a false impression that a species is safe, so that destruction of habitat and wild populations can proceed. Certain recent proposals to breed sea turtles and Spotted Owls (*Strix occidentalis*) in captivity have likely been put forth with exactly this objective in mind.

Preemption of other conservation alternatives is an acute problem when decisions are made to bring all members of a species into captivity before causes of endangerment are well understood. The chances of success in subsequent reintroductions are greatly reduced under such conditions. A decision to bring all Puerto Rican Parrots into captivity in 1972 was fortunately never carried out (Snyder et al. 1987). Research into population-limiting factors has since led to slow recovery of the wild population, whereas captive breeding has yet to become a fully successful enterprise (Wilson et al. 1994).

Ensuring Administrative Continuity

During the past 20 years we have participated in captive-breeding and reintroduction programs for a diverse array of endangered species. The level of success in these programs has depended heavily on the degree of commitment and expertise characterizing program administrators. Yet one of the most alarming features of virtually all these programs has been a high degree of instability in the quality of efforts. In particular, many unintended effects have resulted from personnel changes over the years. Such changes are inevitable and often occur for reasons that have little to do with the goals of maximizing program performance.

Multiple changes in administrative personnel will occur during the lifetimes of many conservation programs because of the often slow rate of recovery of endangered species. For "Millennium arks," the personnel turnover will be truly extraordinary. Captive breeding programs for endangered species are not unique with respect to their susceptibility to variations in administrative quality. However, these programs are vulnerable to the effects of such variations because they are input intensive and because serious mistakes, once made, may be impossible to correct. Complex in situ efforts are also vulnerable to effects of administrative decay. But when straightforward species or habitat protection is adequate for species conservation, in situ efforts can have a significant advantage in long-term stability.

In practical terms, the difficulties in ensuring adequate administrative continuity are among the most serious problems faced by most breeding programs, governmental or private. Yet, this subject has been almost completely ignored (Clark et al. 1994). The general assumption seems to be that programs will always proceed in a rational, goal-maximizing manner. Real-life deviations from this assumption are frequent and should be weighed heavily against presumed benefits of captive breeding in decisions regarding the initiation of captive breeding programs likely to last more than a few years.

Conclusions

The short-term successes in conserving a few endangered species through captive breeding have led to extraordinary enthusiasm for this technique in parts of the conservation community (Rahbek 1993). This enthusiasm has reached an apogee in the "ark" paradigm that envisions preservation of legions of vertebrate species in captivity for up to hundreds of years—to be someday reestablished in the "wild." This view assumes success rates in breeding and genetic/behavioral management in many species that are unattainable, probabilities of successful reintroduction to the wild that are unrealistic, and a sustained availability of resources that is unlikely. Perhaps most unconvincing of all is an unwarranted confidence in the continued viability of human institutions to safeguard species in captivity under social and economic conditions that can be expected to vary from benign to chaotic over the long term. In short, we believe the ark paradigm is fundamentally flawed and diversionary.

The scope of problems inherent in conducting comprehensive captive breeding programs for species recovery, the great expense involved in these programs, and the fundamental limitations of these programs to produce long-term conservation benefits suggest strongly that captive breeding should generally be viewed as a last-resort recovery strategy. In contrast to the basically prophylactic approach to captive breeding taken by the CBSG and by many recovery plans, we believe that captive breeding should not normally be recommended or initiated in recovery efforts before careful field studies have been completed and a comprehensive determination has been made that preferable conservation alternatives are not immediately available and that captive breeding is essential for near-term survival of a species. Captive breeding should not be a long-term conservation strategy and, when adopted as a recovery technique, should always be integrated with simultaneous efforts to maintain, augment, or reestablish wild populations. Although captive breeding does have an important and positive role to play in a small percentage of recovery programs, attempts to use this technique as a panacea uncoupled from conservation efforts for wild populations can be expected to be detrimental. Clearly, every proposal to establish a captive population for recovery merits thorough evaluation and objective peer review.

Captive breeding should not be invoked as a species recovery tool simply because a wild population falls below what may be determined to be a minimum viable size. Such populations may still be far more viable than captive populations given the many problems associated with captive breeding and reintroduction. Although population viability analyses have been used frequently to justify captive breeding, none to our knowledge has ever made rigorous comparisons of the long-term viability of wild and captive populations or acknowledged many of the aforementioned factors affecting the viability of captive populations. In many cases alternative, non-captive approaches may be more effective, economical, and safe than captive approaches in achieving recovery. Usually there is enough time to investigate promising alternatives before initiating captive breeding, and conservation organizations should emphasize such investigations as a high priority.

All recovery programs incorporating either reintroductions of captive-bred stock or translocations of wild animals should incorporate rigorous disease prevention and screening procedures. The disease precautions we advocate for recovery captive breeding populations are restrictive and may be sufficiently expensive to preclude captive breeding as a recovery approach for many species. However, many of the species that have been recommended for recovery captive breeding (Seal et al. 1992) do not merit this approach in the first place. Further, not only disease risks, but also overall costs (e.g., labor, construction, transportation) can generally be minimized by conducting recovery captive breeding programs in countries of origin rather than in ex situ environments in developed nations. Locating captive programs for endangered species within their countries of origin can simultaneously provide a unique foundation for additional, synergistic conservation programs aimed at research, training, public education, and habitat preservation.

In today's era of "animal rights" many zoological institutions are under severe attack and view their own survival as tied closely to their involvement in captive management of endangered species. As long as such institutions limit their efforts to species that truly need captive breeding and ensure that these efforts are properly carried out and closely integrated with protection of wild populations and habitats, we see great benefit in their participation in recovery programs.

Although we believe captive breeding of endangered species for recovery should not be conducted in open multi-species facilities outside of the species' native range, this should not be construed as an anti-zoo orientation. We strongly support the efforts of zoos to establish recovery captive populations in appropriate facilities in countries of origin of endangered species when such programs are advisable and are desired by local governments. Further, we strongly support the efforts of zoos to pursue other "nonrecovery" forms of captive breeding of endangered species; for example, to ensure supplies of animals for exhibition. In addition, we firmly believe that zoological institutions have an important role to play in endangered species conservation through their support of public education, professional training, research, and in situ conservation programs. Many zoological institutions directly support field studies and education programs in both native and foreign countries, and their traditional role as institutions for display of exotic creatures is changing rapidly (Mallinson 1988; Wemmer et al. 1994; Conway 1995; Hutchins et al. 1995). These in situ conservation and education programs may ultimately contribute far more to the overall preservation of biodiversity than breeding programs aimed at single species.

It is no exaggeration to say zoological institutions are one of the major hopes for the future of conservation of biodiversity. At the same time, we fear that by focusing on recovery captive breeding as their central role in conservation, some institutions may fall short of their full conservation potential. It would be tragic if these considerable potentials were frittered away in ill-conceived and expensive attempts to create and maintain captive breeding programs for species that are much better conserved by other approaches.

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Literature Cited

Akçakaya, H. R. 1990. Bald Ibis *Geroaticus eremita* population in Turkey: an evaluation of the captive breeding project for reintroduction. Biological Conservation **51**:225-238.

Allen, W. H. 1994. Reintroduction of endangered plants. BioScience **44**:65-58.

Allendorf, F. W. 1993. Delay of adaptation to captive breeding by equalizing family size. Conservation Biology **7**:416-419.

Anonymous. 1994. Ad hoc meeting to address status of California Condor. Conservation Biology **8**:942.

Arnizaut, A., and R. A. Perez-Rivera. 1991. An epizootic of *Tanaisia bragai* in a captive Population of Puerto Rican Plain Pigeons. Annals of the New York Academy of Sciences **653**:202-205.

Ashton, P. S. 1988. Conservation of biological diversity in botanical gardens. Pages 19-278 in E. O. Wilson, editor. Biodiversity. National Academy Press, Washington, D.C.

Ashton, W. L. G., and J. E. Cooper. 1989. Exclusion, elimination and control of avian pathogens. Pages 31-38 in J. E. Cooper, editor. Disease and threatened birds. Technical publication no. 10. International Council for Bird Preservation, Cambridge, England.

Balmford, A., N. Leader-Williams, and M. J. B. Green. 1995. Parks or arks: where to conserve large threatened mammals? Biodiversity and Conservation **4**:595-607.

Beck, B. B., L. G. Rapaport, M. S. Price, and A. Wilson. 1994. Reintroduction of captive-born animals. Pages 265-284 in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, editors. Creative conservation: Interactive management of wild and captive animals. Chapman and Hall, London.

Belyaev, D. K. 1979. Destabilizing selection as a factor in domestication. Journal of Heredity **70**:301-308.

Brock, M. K., and B. N. White. 1992. Application of DNA fingerprinting to the recovery program of the endangered Puerto Rican Parrot. Proceedings of the National Academy of Sciences (USA) **89**: 11121-11125.

Bush, M., B. B. Beck, and R. J. Montali. 1993. Medical considerations of reintroduction. Pages 24-26 in M. E. Fowler, editor. Zoo and wild animal medicine: current therapy. W. B. Saunders, Philadelphia.

Burton, F. 1993. Captive breeding. Page 12 in K. R. Rough-Moses, editor. National Trust for the Cayman Islands, 1993. Annual report. National Trust for the Cayman Islands, Grand Cayman.

Carpenter, J. W., M. J. G. Appel, R. C. Erickson, and M. N. Novilla. 1976. Fatal vaccine-induced canine distemper virus infection in black-footed ferrets. Journal of the American Veterinary Medical Association **169**:961-964.

Castle, M. D., and B. M. Christensen. 1990. Hematozoa of Wild Turkeys from the midwestern United States: Translocations of Wild Turkeys and its potential role in the introduction of *Plasmodium kempi*. Wildlife Diseases **26**:180–185.

Clark, T. W., R. P. Reading, and A. L. Clarke, Editors. 1994. Endangered species recovery. Island Press, Washington, D.C.

Clubb, S. L. 1992. The role of private aviculture in the conservation of Neotropical psittacines. Pages 117–131 in S. R. Beissinger and N. F. R. Snyder, editors. New World parrots in crisis: solutions from conservation biology. Smithsonian Institution Press, Washington, D. C.

Conway, W. G. 1986. The practical difficulties and financial implications of endangered species breeding programmes. International Zoo Yearbook **24/25**:210–219.

Conway, W. G. 1995. Wild and zoo animal interactive management and habitat conservation. Biodiversity and Conservation **4**:573–594.

Cooper, J. E. 1993. Historical survey of disease in birds. Journal of Zoo and Wildlife Medicine **24**:296–303.

Cromie, R. L., J. L. Stanford, M. J. Brown, and D. J. Price. 1989. A progress report of the project to develop a vaccine against avian tuberculosis. Wildfowl **40**:146–148.

Danielle, A., and N. D. Murray. 1986. Effects of inbreeding in the Budgerigar(*Melopsittacus undulatus*) (Aves: Psittacidae). Zoo Biology **5**:233–238.

Dein, F. J., J. W. Carpenter, G. G. Clark, R. J. Montali, C. L. Crabbs, T. F. Tsai, and D. E. Docherty. 1986. Mortality of captive whooping cranes caused by eastern equine encephalitis virus. Journal of the American Veterinary Medical Association **189**:1006–1010.

Derrickson, S. R., and N. F. R. Snyder. 1992. Potentials and limits of captive breeding in parrot conservation. Pages 133–163 in S. R. Beissinger and N. F. R. Snyder, editors. New World parrots in crisis: solutions from conservation biology. Smithsonian Institution Press, Washington, D. C.

Docherty, D. E., and R. T. Romaine. 1983. Inclusion body disease of cranes: a serological follow-up to the 1978 die-off. Avian Diseases **27**:830–835.

Durrell, L., and J. Mallinson. 1987. Reintroduction as a political and educational tool for conservation. Dodo, Journal of the Jersey Wildlife Preservation Trust **24**:6–19.

Fleming, I. A., and M. R. Gross. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. Ecological Applications **3**:230–245.

Fleming, I. A. 1994. Captive breeding and the conservation of wild salmon populations. Conservation Biology **8**:886–888.

Foose, T. J., and J. D. Ballou. 1988. Management of small populations. International Zoo Yearbook **27**:26–41.

Foose, T.J., and U. S. Seal. 1992. Conservation assessment and management plans: global captive action plans. Section II in Conservation Assessment and Management Plans (CAMP)/Global Captive Action Plans (GCAP) briefing book core materials. International Union for the Conservation of Nature and Natural Resources/Captive Breeding Specialist Group, Apple Valley, Minnesota.

Foose, T. J., N. Flesness, U. S. Seal, B. De Boer, and G. Rabb. 1992. Ark into the 21st century. International Union for the Conservation of Nature and Natural Resources/Captive Breeding Specialist Group, Apple Valley, Minnesota.

Frazer, N. 1992. Sea turtle conservation and halfway technology. Conservation Biology **6**:179–184.

Gough, J. F. 1989. Outbreaks of Budgerigar fledgling disease in three aviaries in Ontario. Canadian Veterinary Journal **30**:672–674.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science **245**:477–480.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1993. Animal translocations and potential disease transmission. Journal of Zoo and Wildlife Medicine **24**:231–236.

Hamilton, M. B. 1994. Ex situ conservation of wild plant species: time to reassess the genetic assumptions and implications of seed banks. Conservation Biology **8**:39–49.

Harris, M. P. 1970. Abnormal migration and hybridization of *Larus argentatus* and *L. fuscus* after interspecies fostering experiments. Ibis **112**:488–498.

Hu, J., and F. Wei. 1990. Development and progress of breeding and rearing giant pandas in captivity within China. Pages 322–325 in J. Hu, F. Wei, C. Yuan, and Y. Wu, editors. Research in progress in biology of the giant panda. Sichuan Publishing House, Sichuan, China.

Hutchins, M., K. Willis, and R. J. Wiese. 1995. Strategic collection planning: theory and practice. Zoo Biology **14**:5–25.

Jacobson, E. R. 1993. Implications of infectious diseases for captive propagation and introduction programs of threatened and endangered species. Journal of Zoo and Wildlife Medicine **24**:245–255.

Johnsson, J. I., and M. V. Abrahams. 1991. Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*): an experimental study. Canadian Journal of Fisheries and Aquatic Sciences **48**:243–247.

Jones, C. G., W. Heck, R. E. Lewis, Y. Mungroo, G. Slade, and T. Cade. 1995. The restoration of the Mauritius Kestrel *Falco punctatus* population. Ibis **137** (Supplement 1):173–180.

Kleiman, D. G. 1989. Reintroduction of captive mammals for conservation. BioScience **39**:152–160.

Knoder, E. 1959. Morphological indicators of heritable wildness in the Turkey (*Meleagrisgallopavo*) and their relation to survival. Pages 116–134 in Proceedings of the first national Wild Turkey symposium. Wildlife Society, Memphis, Tennessee.

Kohane, M. J., and P. A. Parsons. 1988. Domestication: evolutionary change under stress. Evolutionary Biology **23**:31–48.

Lande, R. 1988. Genetics and demography in biological conservation. Science **241**:1455–1460.

Landolf, M., and R. M. Kocan. 1976. Transmission of avian pox from Starlings to Rothschild's Mynahs. Journal of Wildlife Disease **12**: 353–356.

Leader-Williams, N. 1990. Black rhinos and African elephants: lessons for conservation funding. Oryx **24**:23–29.

Leopold, A. S. 1944. The nature of heritable wildness in turkeys. Condor **46**:133–197.

Lewis, J. C. 1990. Captive propagation in the recovery of the Whooping Crane. Endangered Species Update **8(1)**:46–48.

Lyles, A. M., and R. M. May. 1987. Problems in leaving the ark. Nature **326**:245–246.

Mallinson, J. C. 1988. Collaboration for conservation between the Jersey Wildlife Preservation Trust and countries where species are endangered. International Zoo Yearbook **27**:176–191.

Mason, J. W., O. M. Bryndilson, and P. E. Degursz. 1967. Comparative survival of wild and domestic strains of brook trout in streams. Transactions of the North American Fisheries Society **96**:313–319.

Meffe, G. K. 1992. Techno-arrogance and halfway technologies: salmon hatcheries on the Pacific coast of North America. Conservation Biology **6**:350–354.

Merola, M. 1994. A reassessment of homozygosity and the case for inbreeding depression in the Cheetah. Conservation Biology **8**:961–971.

Merton, D., and R. Empson. 1989. But it doesnt'look like a parrot! Birds International **1(1)**:60–72.

Millam, J. R., T. E. Roudybush, and C. R. Grau. 1988. Influence of environmental manipulation and nest-box availability on reproductive success of captive Cockatiels (*Nymphicus hollandicus*). Zoo Biology **7**:25–34.

Miller, B., D. Biggins, C. Wemmer, R. Powell, L. Calvo, L. Hanebury, and T. Wharton. 1990. Development of survival skills in captive-raised Siberian polecats (*Mustela eversmanni*) II: predator avoidance. Journal of Ethology **8**:95–104.

Miller, B., D. R. Reading, and S. Forrest. In press. Prairie night: Recovery of the black-footed ferret. Smithsonian Institution Press, Washington, D.C.

Moyle, P. B. 1969. Comparative behavior of young brook trout of domestic and wild origin. Progressive Fish Culturist **31**:51-59.

Myers, J. H., and M. D. Sabath. 1980. Genetic and phenotypic variability, genetic variance and success of establishment of insect introductions for the biological control of weeds. Pages 91-102 in E.L. Delfosse, editor. Proceedings of the fifth international symposium on the biological control of weeds, 1980, Brisbane. Commonwealth Scientific and Industrial Research Organization, Melbourne.

Myers, S. A., J. R. Millam, T. E. Roudybush, and C. R. Grau. 1988. Reproductive success of hand-raised vs. parent-reared Cockatiels. Auk **105**:536-542.

National Research Council. 1990. Decline of the sea turtles: causes and prevention. National Academy Press, Washington, D.C.

National Research Council. 1992. The scientific bases for the preservation of the Hawaiian Crow. National Academy Press, Washington, D.C.

O'Brien, S. J., and J. F. Evermann. 1988. Interactive influences of infectious disease and genetic diversity in natural populations. Trends in Ecology and Evolution **3**:254-259.

Odum, R. A., and M. J. Goode. 1994. The species survival plan for *Crotalus durissus unicolor*: a multifaceted approach to conservation of an insular rattlesnake. Pages 363-368 in J. B. Murphy, K. Adler, and J. T. Collins, editors. Captive management and conservation of amphibians and reptiles. Contributions to herpetology, vol. 11. Society for the Study of Amphibians and Reptiles, Ithaca, New York.

Partington, C. J., C. H. Gardiner, D. Fritz, L. G. Phillips, Jr., and R. J. Montali. 1989. Atoxoplasmosis in Bali Mynahs (*Leucopsar rothschildi*). Journal of Zoo and Wildlife Medicine **20**:328-335.

Philippart, J. C. 1995. Is captive breeding an effective solution for the preservation of endemic species? Biological Conservation **72**:281-295.

Pullin, A. 1993. Large copper butterfly in England. Re-introduction News **6**:10-11.

Rahbek, C. 1993. Captive breeding—a useful tool in the preservation of biodiversity? Biodiversity and Conservation **2**:426-437.

Ralls, K., and J. Ballou. 1983. Extinctions: lessons from zoos. Pages 164-184 in S. M. Schoenwald-Cox, S. M. Chambers, B. MacBride, and L. Thomas, editors. Genetics and conservation. Benjamin/Cummings, Menlo Park, California.

Seal, U. S., R. Wirth, J. Thomsen, S. Ellis-Joseph, and N. Collar, editors. 1992. Parrots, conservation assessment and management plan (CAMP) workshop report, draft review edition. International Council for Bird Preservation/International Union for the Conservation of Nature and Natural Resources/Captive Breeding Specialist Group, Cambridge, United Kingdom.

Seal, U. S., S. A. Ellis, T. J. Foose, and A. P. Byers. 1993. Conservation assessment and management plans (CAMPs) and global action plans (gcaps). Captive Breeding Specialist Group Newsletter **4(2)**: 5-10.

Setchell, K. D. R., S. J. Gosselin, M. B. Welsh, J. O. Johnston, W. F. Balistreri, L. W. Kramer, B. L. Dresser, and M. J. Tarr. 1987. Dietary estrogens—a probable cause of infertility and liver disease in captive cheetahs. Gastroenterology **93**:225-233.

Shima, A. L., and K. G. Osborn. 1989. An epornitic of *Salmonella typhimurium* in a collection of lories and lorikeets. Journal of Zoo and Wildlife Medicine **20**:373-376.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. Annual Review of Ecology and Systematics **19**:473-511.

Snyder, B., J. Tahilsted, B. Burgess, and M. Richard. 1985. Pigeon herpesvirus mortalities in foster-reared Mauritius Pink Pigeons. Proceedings of the American Association of Zoo Veterinarians 1985:69-70.

Snyder, N. F. R., S. E. Koenig, J. Koschmann, H. A. Snyder, and T. B. Johnson. 1994. Thick-billed Parrot releases in Arizona. Condor **96**: 845-862.

Snyder, N. F. R., and H. A. Snyder. 1989. Biology and conservation of the California Condor. Current Ornithology **6**:175-263.

Snyder, N. F. R., J. W. Wiley, and C. B. Kepler. 1987. The parrots of Luquillo; natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles.

Soulé, M. E., M. Gilpin, W. Conway, and T. Foose. 1986. The millennium ark: how long a voyage, how many staterooms, how many passengers? Zoo Biology **5**:101-114.

Spurway, H. 1955. The causes of domestication: an attempt to integrate some ideas of Konrad Lorenz with evolution theory. Journal of Genetics **53**:325-362.

Sterling, E. J. 1993. Behavioral ecology of the aye-aye (*Daubentonia madagascariensis*) on Nosy Mangabe, Madagascar. Ph.D. dissertation. Yale University, New Haven, Connecticut.

Swain, D. P., and B. E. Riddell. 1990. Variation in agonistic behaviour between newly-emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences **47**:566-571.

Svitalsky, M., J. Vahala, and P. Spala. 1993. Breeding experience with northern white rhinos (*Ceratotherium simum cottoni*) at zoo Dvur Kralove. Pages 282-286 in O. A. Ryder, editor. Rhinoceros biology and conservation. Zoological Society of San Diego, San Diego.

Tear, T. H., J. M. Scott, P. H. Hayward, and B. Griffith. 1993. Status and prospects for success of the Endangered Species Act: a look at recovery plans. Science **262**:976-977.

Thorne, E. T., and E. S. Williams. 1988. Disease and endangered species: the black-footed ferret as an example. Conservation Biology **2**: 66-74.

Tudge, C. 1992. Last animals at the zoo: How mass extinction can be stopped. Island Press, Washington, D.C.

Welsh, R. D., R. W. Ely, and R. J. Holland. 1992. Epizootic of *Yersinia pseudotuberculosis* in a wildlife park. Journal of the American Veterinary Medical Association **201**:142-144.

Wemmer, C., R. Rudran, F. Dallmeier, and D. E. Wilson. 1994. Training developing country nationals is the critical ingredient to conserving biological diversity. BioScience **43**:762-767.

Wiemeyer, S. N., J. M. Scott, M. P. Anderson, P. H. Bloom, and C. J. Stafford. 1988. Environmental contaminants in California Condors. Journal of Wildlife Management **52**:238-247.

Wiley, J. W., N. F. R. Snyder, and R. S. Gnam. 1992. Reintroduction as a conservation strategy for parrots. Pages 165-200 in S. R. Beissinger and N. F. R. Snyder, editors. New world parrots in crisis: solutions from conservation biology. Smithsonian Institution Press, Washington, D.C.

Willis, K., and R. J. Wiese. 1993. Effect of new founders on retention of gene diversity in captive populations: a formalization of the nucleus population concept. Zoo Biology **12**:535-548.

Wilson, M. H., C. B. Kepler, N. F. R. Snyder, S. R. Derrickson, F. J. Dein, J. W. Wiley, J. M. Wunderle, Jr., A. E. Lugo, D. L. Graham, and W. D. Toone. 1994. Puerto Rican Parrots and potential limitations of the metapopulation approach to species conservation. Conservation Biology **8**:114-123.

Wolff, P. L., and U. S. Seal. 1993. Implications of infectious disease for captive propagation and reintroduction of threatened species. Journal of Zoo and Wildlife Medicine **24**:229-230.

Woodford, M. H., and P. B. Rossiter. 1994. Disease risks associated with wildlife translocation projects. Pages 178-200 in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, editors. Creative conservation: Interactive management of wild and captive animals. Chapman and Hall, London.

Worley, M. B. 1993. Molecular biology and infectious disease: present and future trends in diagnosis. Journal of Zoo and Wildlife Medicine **24**:336-345.

Yamamoto, J. T., K. M. Shields, J. R. Millam, T. E. Roudybush, and C. R. Grau. 1989. Reproductive activity of force-paired Cockatiels (*Nymphicus hollandicus*). Auk **106**:86-93.