Puerto Rican Parrots and Potential Limitations of the Metapopulation Approach to Species Conservation

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Abstract: *Population viability analyses for a number of endangered species have incorporated a metapopulation approach. The risk assessments of these viability analyses have indicated that some extant populations should be subdivided into numerous subgroups with exchange of individuals among them in order to reduce the chance of catastrophic loss of the species. However, routine application of a policy of extensive subdivision may have detrimental consequences for certain endangered species. We examine the Puerto Rican Parrot as a case history in which this policy is ill-advised. In 1989, a population viability analysis was conducted for the*

Las cotorras portorniqueñas y las limitaciones potenciales de la estrategia de metapoblaciones aplicada a la conservación de especies

Resumen: *Los análisis de viabilidad de poblaciones hechos para un gran número de especies en peligro de extinción ahora tienen un enfoque de metapoblación. Para reducir las probabilidades de pérdidas catastróficas de individuos de una especie, poblaciones existentes se subdividen en numerosos subgrupos; ésto se hace de acuerdo a los resultados de los análisis de riesgo que son parte integral del enfoque de análisis de viabilidad de poblaciones. Sin embargo, la subdivisión contíinua y rutinaria de poblaciones de especies en peligro de extinción puede ser detrimental para la sobrevivencia de la especie. Examinamos al caso de la Cotorra Puertorriqueña dónde este tipo de enfoque no es recomen-*

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parrot. The document recommended subdivision of the existing small captive flock into three groups. One of these captive flocks would consist of individuals transferred to a multi-species facility in the continental United States. Subsequently, individuals from this facility would be exchanged with the insular captive population(s) and the relict wild flock. For two reasons, implementation of this recommendation might have led to serious repercussions. First, this parrot, like many endangered species, has gone through a genetic bottleneck and may have a heightened susceptibility to disease. Multi-species facilities are a high-risk environment favoring the transmission of pathogens, especially when the facilities are located outside the natural ranges of a particular species. Second, the parrot is a K*-selected species for which mate selection is idiosyncratic. This type of species often proves difficult to breed in captivity in small groups. Part of the problem in mate selection may be reduced by a policy allowing frequent transfers of individuals among facilities, but such movements increase the chances of spreading disease in the metapopulation. Thus, population viability analyses need to acknowledge that proliferation of captive subgroups accompanied by exchanges of individuals can in themselves carry substantial risks that must be weighed against the presumed benefits of subdivision.*

dable. En el 1989, un análisis de viabilidad poblacional se efectuó para la Cotorra Puertorriqueña. Como resultado del análisis se recomendó la subdivisión en tres grupos de la pequeña población cautiva existente. Se recomendó, además, transferir uno de los tres grupos a una facilidad con múltiples especies en los Estados Unidos de América. Subsiguientemente, individuos de esta facilidad serían intercambiados con las poblaciones cautivas en Puerto Rico y con la población de cotorras aún sobreviviendo bajo condiciones naturales. Hay dos razones por las cuales tales recomendaciones podrian haber repercutido seriamente sobre la cotorra. En primer lugar, esta especie, como muchas otras en peligro de extinción, ha atravesado por un cuello de botella genético y como resultado de esto su suceptibilidad a enfermedades ha incrementado. Facilidades con múltiples especies son ambientes de alto riesgo para especies como la cotorra pues en ellos se favorece la transmisión de patógenos, especialmente cuando los facilidades están localizadas lejos del ambiente natural de especies particulares. En segundo lugar, la cotorra es una especie tipo K *para la cuál la selección de parejas es idiosincrática. Este tipo de especie es generalmente difícil de propagar en cautiverio particularmente cuando las poblaciones son pequeñas. Parte del problema de selección de parejas se puede aliviar intercambiando frecuentemente individuos entre facilidades, pero tal estrategia aumenta el riesgo de transmisión de enfermedades entre las metapoblaciones. Por lo tanto, el análisis de viabilidad de poblaciones debe considerar que la proliferación de subgrupos cautivos acompañados por el intercambio continuo de individuos en esos subgrupos, por su cuenta, conlleva riesgos sustanciales que se deben contraponer ante los presuntos beneficios de la subdivisión de las poblaciones.*

Introduction

A primary objective of applied conservation biology is to minimize extinction rates of threatened species (Goodman 1987; Quinn & Hastings 1987). This orientation led to defining minimum viable populations and to incorporating the metapopulation concept as a frame of reference into species conservation (Shaffer 1985; Simberloff 1988).

Gilpin and Soulé (1986) introduced the process known as population viability (sometimes vulnerability) analysis (PVA) to estimate minimum viable populations and to plot conservation strategies for endangered species. The PVAs produced to date have involved both intrinsic population characteristics (morphology, physiology, reproduction, disease resistance, mobility, behavior, etc.) and environmental constraints (habitat quantity and quality, interacting species, disease vectors, etc.). These features may allow estimation of extinction probabilities and development of strategies to minimize these probabilities. As noted by Shaffer (1990), PVA is an emerging technique of risk analysis that does not as yet have a well-developed methodology or widely accepted standards. The PVA process has been applied to about 46 species, including a variety of threatened vertebrates, invertebrates, and plants (U. S. Seal, personal communication).

Recently, a metapopulation approach has been incorporated into many PVAs (for example, the 1989 Florida Panther Viability Analysis and Species Survival Plan and the 1989 Puerto Rican Parrot PVA). For wild populations, a metapopulation is a complex of interdependent subpopulations affected by recurrent extinctions and linked by recolonization from one or more large reservoir populations (Murphy et al. 1990). For many endangered species, the PVA process has been expanded to include wild and captive subpopulations (Lacy et al. 1989; Seal & Lacy 1989).

To reduce chances of catastrophic loss of all members of an endangered species and to counter genetic drift, Lacy (1987) recommended that managers subdivide a managed population into numerous breeding subgroups that exchange a few individuals per generation. For species with small total populations, the subdivisions can involve very small numbers of individuals in each subpopulation—for example, as few as 12 Puerto Rican Parrots (Lacy et al. 1989).

The costs of dividing wild populations into small subpopulations involve an increased probability of extinction due to demographic stochasticity and a possible loss of genetic variation. If members of each subpopulation reproduce, these costs can theoretically be mitigated in captivity by regularly exchanging individuals among facilities or sites (in the wild). However, blanket application of a metapopulation approach to species conservation can be detrimental for certain endangered species, especially for species with a high susceptibility to diseases or with difficulty of breeding in small captive groups. In this report, we address these two factors for optimal management of endangered species in captivity, with special reference to the endangered Puerto Rican Parrot (*Amazona vittata*).

Disease

Disease can play a major role in the conservation of endangered species, as evidenced by a canine distemper epizootic which led to the extirpation of the black-footed ferret (*Mustela nigripes*) in the wild (Thorne & Williams 1988). Endangered species may often have heightened susceptibility to disease because of reduced genetic variation in small populations (O'Brien et al. 1985; Watkins et al. 1990) and because many endangered species (especially insular species) occur in isolated populations without previous exposure to certain pathogens (van Riper et al. 1986; Cooper 1989; Jenkins et al. 1989). This heightened susceptibility to disease is often apparent when endangered species are compared with closely related but nonendangered species. For example, the endangered Whooping Cranes (*Grus americana*) at the Patuxent Wildlife Research Center have been much more susceptible than the Sandhill Cranes (*G. canadensis*) to coccidia and viral encephalitis (Dein et al. 1986).

Snyder et al. (1985) reported nestling mortalities from herpesvirus infections of the endangered Mauritius Pink Pigeon (*Columba mayeri*) fostered under domestic pigeons (*C. livia*) at the Rio Grande Zoo in Albuquerque. The foster pigeon flock apparently had been free of disease for several years. Four fertile Mauritius Pink Pigeon eggs were fostered to the surrogate birds. However, latently infected foster pigeons shed herpesvirus during the reproductive period, and each of the Mauritius Pink Pigeon hatchlings died suddenly at 5 to 11 days of age. No deaths among nestling domestic pigeons in the foster flock were due to viral infection. The Mauritius Pink Pigeons seemed to have had no previous experience with this virus.

The transfer of live animals or eggs to non-native areas always increases the risk of exposing immigrants to pathogens to which they are not adapted and the risk of spreading pathogens from one area to another (Ashton & Cooper 1989; Gaskin 1989). For example, O'Brien et al. (1985) described the spread of a coronavirus throughout a cheetah (*Acinonyx jubatus*) colony. These authors attributed the cause to a clinically healthy female transferred to Wildlife Safari. Despite intensive therapy, this female and 17 other cheetahs died. O'Brien et al. (1985) suggested that a dearth of genetic variation rendered this colony extremely susceptible.

Gaskin (1989) suggested that congregation of a diverse array of species from all around the world in quarantine facilities and large, multi-species holdings in zoos, private collections, and the pet trade is one reason captive psittacines are plagued with so many diseases. These multi-species congregations have provided enhanced opportunities for the transmission of infectious agents.

Quarantine, a common practice in the transfer of live animals to new locations, does not guarantee that an individual is free of diseases. Many disease agents are not necessarily fatal on contact but can remain latent in carriers and be shed intermittently, particularly under stress. Carriers can harbor certain diseases for their entire lives and may transmit infections to their offspring. The most disturbing fact is that carriers of some disease agents can be asymptomatic. Such is the case with a psittacine herpesvirus known as Pacheco's disease (Gaskin 1989), and with a number of other avian diseases.

Shima and Osborn (1989) identified a pair of newly acquired Red-Collared Lorikeets (*Trichoglossus haematodus rubritorquis*) as the "point source" of an epornitic of *Salmonella typhimurium* in the San Diego Zoo collection of lories and lorikeets. Seven birds, representing six species, died. The originally infected pair was imported from an Australian zoo, went through standard federal quarantine, and then a 30-day quarantine at a holding facility at the San Diego Wild Animal Park before being introduced into the collection at the zoo. Routine screening failed to identify the problem during quarantine.

The purpose of most zoos is to display animals, and many species are housed in close proximity for viewing by the public. To replace animals that die and to diversify collections for public viewing, zoos continually acquire new individuals and species from around the world. In part, because these animals often come from aggregations of species in quarantine or from other facilities, zoos may be high-risk environments that favor transmission of pathogens. Not surprisingly, many epizootics have been documented in zoological facilities (see Montali et al. 1975*a*; May 1988; Thorne & Williams 1988; Cooper 1989; Derrickson & Snyder 1992).

For threatened birds that might be highly susceptible to diseases and yet are in need of captive propagation, Derrickson and Snyder (1992) recommended the following principles:

(1) Facilities should, whenever possible, be located in the species' natural range.
(2) The species should be housed in two or three geographically isolated, single-species facilities.
(3) The facilities should be staffed by individuals who are not simultaneously caring for other captive birds.
(4) As much as possible, facilities should be in areas free from arthropod vectors and feral populations of exotic birds.
(5) Established husbandry protocols should emphasize disease prevention.

These precautions do not preclude the involvement of zoological institutions in breeding of endangered species that are susceptible to diseases, but they emphasize proper locations and carefully controlled conditions. Likewise, Kennedy-Stoskopf (1989) pointed out that an appropriate environment and good husbandry practices are essential to limiting infectious diseases in captive situations.

Recovery programs for endangered species increasingly include augmenting or reestablishing wild populations with captive individuals or with wild, translocated conspecifics. If either type of individual harbors pathogenic organisms, relict wild populations can be severely jeopardized. For example, many reintroduced populations of Wild Turkeys (*Meleagris gallopavo*) in the U.S. are infected with *Plasmodium kempi,* a hematozoan parasite that appears to have originated from the translocation of infected birds (Castle & Christensen 1990). In a like manner, there is convincing evidence that a movement of rabies up the East Coast was initiated by the translocations of infected raccoons from endemic areas in Florida and Georgia (Nettles et al. 1979). Similarly, the upper respiratory disease in wild desert tortoises (*Xerobates agassizii*) is believed to stem from a probable release of infected pet (or captive-held) tortoises (Anonymous 1989; Jacobson & Gaskin 1990). This disease now threatens the species.

Infectious and parasitic diseases can cause premature death in wild populations (Scott 1988; Cooper 1989). Fatal diseases are notoriously difficult to detect in wild animal populations because sick and dead individuals commonly go unrecovered, in part because they are taken quickly by predators and scavengers (Balcomb 1986; Scott 1988; Linz et al. 1991). Even when a causative agent can be identified in a diseased wild population, treatment is often impractical, particularly if species are difficult to catch or easily stressed by handling or if practical means of treatment are unknown.

Furthermore, disease is most likely to affect a population without previous contact with the pathogen. For example, as noted by Cooper (1989), if the herpesvirus that afflicted the Pink Pigeons in the Rio Grande Zoo had been introduced into the wild Pink Pigeon population in Mauritius, results could have been disastrous. With good reason, Ritchie et al. (1989) stressed that, because of the widespread movement of birds in the pet trade, the risks of introducing highly virulent viruses into wild populations of endangered psittacine species are substantial.

Besides causing premature mortality, introduction of infected captive animals into the wild can also reduce reproduction of wild populations. For example, Hudson (1986) found that reproduction in Red Grouse (*Lagopus scotius*) can be reduced by the nematode (*Trichostrongylus tenuis*). Similarly, Saumier et al. (1986) found that captive American Kestrels (*Falco sparverius*) infected with the parasite *Trichinella pseudospiralis* had severely reduced reproductive success compared with control birds. Infected pairs initiated laying later, laid smaller clutches, and hatched fewer eggs than controls. Identifying an infection, rather than some other factor, as the actual cause of low reproductive success in a wild population is difficult.

Because some avian pathogens can be transmitted in eggs, one cannot avoid transport of pathogens by limiting movements of animals to the egg stage. The bacterium *Salmonella pullorum* can spread from a parent flock via the egg to chicks by true transovarian vertical transmission (Ashton & Cooper 1989). Other avian pathogens can also enter eggs as they cool following surface contamination of the shell (Ashton & Cooper 1989). Vertical transmission is also known to occur with avian leukosis virus, reticuloendotheliosis, adenoviruses, and *Mycoplasma* spp. (Reece 1989). If an infected embryo does not die, infection of newly hatched chicks may occur and spread throughout a captive flock.

Because novel pathogens or their vectors can be spread with increasing ease in the modern world, Cooper (1989) made an urgent plea for minimizing the spread of infectious diseases from one locality to another. As Ashton and Cooper (1989) pointed out, exclusion of an avian pathogen is much easier than its elimination.

Elimination of a disease requires that it is well defined; that it can be easily diagnosed or detectable by a simple, cheap, and rapidly applied test (which is often not available); and that it can be eradicated. But understanding of many diseases, especially avian diseases, is still far from perfect. Part of the difficulty stems from the sheer number of species from all over the world that are involved. Host ranges are unknown for some diseases such as psittacine beak and feather disease, and causative agents are still unknown for others such as psittacine proventricular dilatation syndrome (parrot wasting disease) and internal papillomatous disease. Of the many infectious agents, Gaskin (1989) reported that viruses are the most troublesome mainly because they can occur in epornitic proportions with little possibility of chemotherapeutic intervention.

Once certain pathogens become established in a facility, they can be extremely difficult to control or eliminate. One such disease that has repeatedly plagued zoological and private collections and the poultry industry is avian tuberculosis. This disease affects a wide variety of avian taxa, and it is readily spread by fecal contamination of substrates, feed, or water sources, and possibly also vertically through egg contamination (Montali et al. 1978). Genetic factors can also play a role in transmission (Cromie et al. 1991). Control or eradication of this disease is particularly difficult because the causative bacillus, *Mycobacterium avium,* can remain viable in the soil for years, and because reliable methods to diagnose and treat the disease in live animals remain unavailable. Traditional eradication includes the elimination of the entire collection and either the replacement of existing substrates, the destruction of the entire facility, or movement of the facility to a new site (Montali et al. 1975*b;* Beehler 1990). Such measures obviously entail severe financial, biological, and ethical costs (particularly when dealing with endangered and threatened species), and do not preclude accidental reinfection. Controlling the spread of avian tuberculosis among facilities or between captive and wild populations clearly will not be possible until efficient and accurate diagnostic techniques become available to detect the disease in live animals. Unfortunately, avian tuberculosis has been detected post-mortem in several endangered species, and this insidious disease represents a substantial threat to many ongoing breeding and reintroduction programs.

Polyomaviruses, which are significant pathogens of psittacines, are also resistant to inactivation. For example, Gough (1989) reported on an aviary in which an outbreak of a Budgerigar fledgling disease occurred. After the initial outbreak, breeding operations were curtailed for eight months, but young continued to die when breeding was resumed. The entire aviary was depopulated, fumigated with formaldehyde gas, and left vacant for seven months. Then new breeding stock was purchased from an aviary presumably free of the disease. Despite these massive efforts to eliminate the disease, it soon broke out again.

Likewise, Thorne and Williams (1988) reported that canine parvoviral enteritis, a very contagious infectious virus of canids, is resistant to environmental inactivation. Apparently carrier wolves may have been the source of this virus, which caused mortalities among maned wolves (*Chysocyon brachyurus*) both at the San Antonio Zoo (Fletcher et al. 1979) and at the National Zoological Park (Mann et al. 1980).

In summary, because of the slow-acting but nevertheless lethal or debilitating nature of many pathogens, because of the difficulties in detecting the presence of many pathogens in asymptomatic carriers, because of the widespread movement of animals carrying pathogens through captive-breeding collections around the world, because of the heightened susceptibilities of many endangered species to disease, and because of severe risks of contamination of wild populations of endangered species by infected individuals from captivity, it is questionable that extensive subdivision of captive populations of endangered species, especially in multispecies facilities, represents a risk-reduction strategy rather than a risk-enhancement strategy. This is especially true when movements between subpopulations are routinely required to meet genetic and demographic management objectives. Presumably, many of the risks of disease can be greatly reduced if subdivision of captive populations is limited to single-species facilities within the natural range of the endangered species, and if personnel serving the facilities practice rigorous disease prevention measures, including avoidance of contact with other animals that may be harboring disease agents.

Poor Reproduction of Small Populations Housed in Captivity

The productivity of many species in captivity is affected strongly by population size. In many colonial species, social facilitation is a necessary element for reproduction. For this reason, flamingos and many other colonial waterbirds such as storks, ibises, and spoonbills, usually do not breed in captivity in small groups (Kear & Palmes 1980; Luthin et al. 1985).

For many endangered species, obtaining adequate levels of reproduction in captivity poses difficulties. For species with idiosyncratic mate selection, subdivision of an already small population reduces the number of possible pairings at any one site and therefore the overall productivity of the species.

In many large psittacines, reproduction occurs in only a small fraction of a captive population, and success in captive breeding seems to depend on providing birds with an ample array of potential mates. Even with numerous trials with potential mates, many birds remain nonreproductive, presumably because of their failure to find compatible partners among the available choices. The psittacine literature is rife with examples of the contortions aviculturists have been through to obtain compatible pairs. Even in psittacines, such as Cockatiels (*Nymphicus hollandicus*), that breed relatively freely in captivity, forced pairing commonly results in much less successful reproduction than free mate choice (Yamamoto et al. 1989). The spontaneous choice of mates seems to be crucial for successful reproduction in many avian species, such as Canvasbacks (*Aythya valisineria*) (Bluhm 1985) and Whooping Cranes (Kepler 1978).

With species in which formation of compatible pairs is especially difficult, extensive subdivision of captive populations can pose significant impediments to securing sustained reproduction and meeting genetic management objectives. Both of these problems can be mitigated only by extensive and sometimes expensive transfers of individuals among facilities. Such movements, however, can greatly increase the chance of spreading disease among subpopulations and can increase the vulnerability of the entire metapopulation to disease.

Thus, the perceived reduction of risk from splitting a captive population to prevent loss of an entire genome to some site-specific catastrophe, such as fire, disease, tornados, or local wars, must be balanced against the potential increase in disease exposure and decrease in reproductive potential that may result from subdivision. Viable or optimal group size varies greatly from species to species.

A Case Study: The Puerto Rican Parrot

The Puerto Rican Parrot was abundant and widespread on the islands of Puerto Rico, Culebra, and Vieques. By the late 1960s, it was reduced to a tiny remnant population in the Luquillo Experimental Forest, also known as the Caribbean National Forest. This reduction was caused by a variety of factors, including habitat destruction, capture for pets, and killing for food and protection of crops (Snyder et al. 1987). The wild population reached a low point of 13 birds at the beginning of the 1975 breeding season. Since then it has recovered at a low to moderate rate, reaching a high of 45–47 individuals after the 1989 breeding season. This increase was a result of identification and reduction of several limiting factors affecting the wild population, and of fostering captive-reared birds into wild nests. Meanwhile, a captive population was started in the early 1970s largely through removal of eggs from wild nests, and reached a total of 58 individuals by January 1993 (A. Valido, personal communication).

Although successful captive breeding has been achieved in all years since 1979, the number of breeding pairs has remained low in both wild and captive flocks, averaging about four pairs in each flock. The captive flock is in a single facility within the natural range of the wild population in the Luquillo Experimental Forest. With the exception of captive Hispaniolan Parrots (*Amazona ventralis*) brought in for surrogate studies, the aviary has been essentially closed to importation of other avian species. No significant disease problems have occurred at the facility in the 20 years of its existence.

A second aviary for the species, about 100 km distant, has recently been completed. The site of this second aviary is in the Rio Abajo Commonwealth Forest, which has been acknowledged to be the best location to reestablish a second wild population of the species (U.S. Fish and Wildlife Service 1987).

In June of 1989, the U.S. Fish and Wildlife Service hosted the Captive Breeding Specialist Group of the International Union for the Conservation of Nature and Natural Resources in a PVA on the Puerto Rican Parrot. The PVA report made several recommendations for management of wild and captive flocks, but most notably it advocated the near-term splitting of the captive flock into three parts: the existing Luquillo Aviary in the Luquillo Experimental Forest, the second aviary in Rio Abajo, and a third aviary at some mainland zoo in the United States (Lacy et al. 1989). Ultimately, the PVA recommended the establishment of some 10 captive flocks in various locations, including zoos. These recommendations were based on the application of the metapopulation concept.

The principal justifications offered for sending birds to a mainland zoo were: (1) enhanced reduction of risks from catastrophe, and (2) enhancement of captive reproduction utilizing the resources and expertise at a mainland zoo. The 12 birds recommended for shipment to a mainland zoo were all birds that had not bred as yet in captivity.

The primary threat to both wild and captive populations of the Puerto Rican Parrot has long been perceived to be a major hurricane disaster. By 1989, the last wild habitat of the species had been spared any major hurricane for over 50 years. The effects of a major storm were difficult to predict but were perceived to be significant for both wild and captive flocks, and a consensus has long existed that establishment of a second captive flock and a second wild flock as soon as practical would be best.

Consensus on the advisability of starting a third captive flock, especially one in a mainland zoo location, has been more elusive. Debate on this issue occupied the greater part of 1990 and centered on the two major issues raised in the earlier part of this report: disease risks and projected effects on reproduction. The Puerto Rican Parrot is perhaps a classic example of a species for which high disease susceptibility is predicted. As a member of the Psittacidae, it is a potential host of more than 30 known diseases and potential disease syndromes. Moreover, it is a highly endangered, insular species that has been in a genetic bottleneck for nearly 25 years, a period during which the number of breeding pairs has been low, very likely resulting in a high degree of relatedness and reduced genetic diversity among surviving individuals.

Opponents of the move of birds to a mainland zoo pointed out that a variety of psittacine diseases are very difficult to detect, yet are widespread in mainland zoos and could potentially be spread to captive and wild flocks in Puerto Rico if interchanges of birds were carried out. Conversely, if interchanges were not carried out, it was difficult to see how a mainland zoo flock would have any conservation value for the existing wild population or for a prospective new wild population.

Of special concern, the mainland zoo recommended to host Puerto Rican Parrots has had recurrent cases of avian tuberculosis, a disease that is very difficult to detect in carriers and extremely difficult to eradicate from a facility. Furthermore, this facility maintained a diverse, multi-species psittacine collection and, as a result, the risk of Puerto Rican Parrots contacting other diseases in this facility appeared to be substantial. Opponents of the move suggested that it would be wiser to export the expertise of a mainland zoo to facilities in Puerto Rico rather than to move birds to such a mainland environment. This position was ultimately upheld by the U.S. Fish and Wildlife Service as a result of consultations with its own veterinary experts.

Of equal concern were the potential effects on reproduction from subdividing the captive flock three ways. The captive flock had never supported more than six successful breeding pairs, despite major efforts to establish compatible pairings and despite the fact that surrogate Hispaniolan Parrots had been bred much more successfully at the same facility, using the same techniques. Production of captive young Puerto Rican Parrots has rarely exceeded six individuals in a year, despite experimentation with a variety of husbandry techniques.

What would be the projected effects of splitting the existing captive flock three ways? Clearly, the choices for trying new pairings or allowing maturing birds to select mates would be greatly reduced for each facility from what is now possible. This could conceivably result in a failure to achieve any successful new pairings in any facility. This expectation is based on a track record of needing more than a dozen individuals to form each new productive pair. If, indeed, the major problem in captive reproduction of this species is achieving compatible pairs, a three-way split of the existing captive population could have severe consequences.

Other possible causes of low captive production of the Puerto Rican Parrot likely exist, but the potential importance of these other causes must always be viewed against the consistently successful captive production of Hispaniolan Parrots at the same facility using the same diet and techniques as with the Puerto Rican Parrot. In any event, a case has yet to be made that solutions to the low captive reproduction of Puerto Rican Parrots can be found any more easily in a mainland environment than within the natural range of the species.

Almost as if to test the strength of conservation strategies under debate, Puerto Rico was directly hit by a major storm, Hurricane Hugo, in September of 1989. This hurricane caused massive damage to the remnant habitat of the Puerto Rican Parrot. The parrot aviary, however, survived almost completely unscathed, and with no loss of birds. The wild population was reduced from 45–47 birds to about 25 birds. Interestingly, parrot breeding resumed in 1990. In 1991, a record six pairs of parrots bred in the wild, the highest total since the 1950s. The next year, these six pairs fledged a record of 11 young, and the post-breeding population estimate was between 34 and 37 parrots (A. Valido, personal communication). It presently appears that chances for a resumption of sustained recovery of the wild population are relatively good. Evidently, the amount of risk attributed to a major storm can be overestimated, to both captive and wild populations.

How many subpopulations of the Puerto Rican Parrots are needed at the present time? Clearly the answer to this question is crucially dependent on how many birds are available and on how many birds constitute a critical mass for successful reproduction. Splitting either the existing wild flock or the existing captive flock carries penalties to these flocks that must be weighed against the benefits. The existing two subpopulations have just come through a major environmental disaster in relatively good shape, which should perhaps temper enthusiasm for splitting them up. Had the wild population been only half as large at the time the storm hit, things could look much worse now than they do.

In our view, the wild flock has shown a surprisingly encouraging resilience and ability to increase over the past two decades (at a rate very similar to the recovery of the wild population of Whooping Cranes). Now it has also shown an encouraging survival through a major storm. We believe that preserving the integrity of this population represents the highest priority in future efforts to preserve the species.

In view of the long history of relatively poor performance of the species in captivity, conservation efforts should not be skewed toward large-scale proliferation of captive populations; instead, the fruits of captive production in the near term should be used largely to bolster the existing wild population. Once that population reaches perhaps 70 to 100 individuals, it may obtain a fairly comfortable status with respect to future hurricanes, and it will become important to begin the establishment of a second wild flock.

Meanwhile, we believe that establishment of a second captive flock in Rio Abajo represents a reasonable strategy, but it should not take place at the expense of the productivity of the existing captive or wild subpopulations. This second aviary should be established with current nonbreeders and juveniles from the existing captive flock. No attempts to establish a second wild flock should be made until the existing wild flock exceeds 70 birds, because such efforts would conflict with bolstering the extant wild flock as quickly as possible while it is still at a critically low level. We see no clear advantage in establishing a third captive flock at the present time.

Conclusions

The overriding goal of securing wild populations can sometimes be forgotten in the recent climate of enthusiasm for captive breeding. The primary rationale usually offered for establishing multiple captive populations is one of risk reduction from catastrophe. Unfortunately, it is not often acknowledged that proliferation of captive populations itself carries significant risks, especially with respect to disease vulnerability and reproductive penalties.

The recent case history of the critically endangered Puerto Rican Parrot indicates that even major catastrophes can have relatively limited effects on some populations. This experience underscores the need for incorporating more rigorous information on the species' ecology into genetic models and into concepts of metapopulations. Species and populations have resiliency mechanisms that may be as important as genetic make-up in their day-to-day survival. Therefore, decisions on their management must balance ecological and genetic arguments.

The recovery potential of some species may also depend on critical-mass effects that argue against oversplitting populations. When subdivision involves moving endangered species into non-native areas, it places them in close proximity to potential vectors of new diseases. The risks involved cannot be rigorously quantified in magnitude, but they appear to be well worth avoiding when alternatives exist. The consequences of mistakes can easily prove fatal to species.

We wish to make perfectly clear that we do not oppose an important role for zoological institutions in the conservation of endangered species, and in fact we strongly support such a role. Much remains to be improved, however, regarding the precautions taken in breeding endangered species in captivity, particularly in disease prevention and control. Attempts to house species that are arguably sensitive to disease in ex situ multi-species environments are generally unwise, and the should be replaced by a preference for breeding endangered species in situ in closed single-species facilities operating under rigorous disease-prevention protocols. While this approach is in some cases more expensive, such is not always the case, especially considering the costs of routine international transport in ex situ approaches. Furthermore, the benefits of in situ programs that involve further communities in the conservation of their native fauna can be as substantial as the benefits in reducing unnecessary risks of exposure to disease.

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Literature Cited

Anonymous. 1989. Emergency action taken to protect the desert tortoise. Endangered Species Technical Bulletin **14**:1, 5–6.

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. Cambridge, England.

Balcomb, R. 1986. Songbird carcasses disappear rapidly from agricultural fields. Auk **103**:817–820.

Beehler, B. A. 1990. Management of *Mycobacterium avium* in a mixed species aviary. Pages 125–129 in Proceedings of the American Association of Zoo Veterinarians.

Bluhm, C. K. 1985. Mate preferences and mating patterns of Canvasbacks (*Aythya valisineria*). Ornithological Monographs **37**:45–56.

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

Cooper, J. E. 1989. The role of pathogens in threatened populations: An historical review. Pages 51–61 in J. E. Cooper, editor. Disease and threatened birds. Technical publication No. 10. , Cambridge, England.

Cromie, R. L., M. J. Brown, D. J. Price, and J. L. Stanford. 1991. Susceptibility of captive waterfowl to avian tuberculosis. Tubercle **72**:105–109.

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.

Fletcher, K. C., A. K. Eugster, R. E. Schmidt, and G. B. Hubbard. 1979. Parvovirus infection in maned wolves. Journal of the American Veterinary Medical Association **175**:897–900.

Gaskin, J. M. 1989. Psittacine viral diseases: A perspective. Journal of Zoo and Wildlife Medicine **20(3)**:249–264.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: Processes of species extinction. Pages 19–34 in M. E. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Goodman, D. 1987. How do any species persist? Lessons for conservation biology. Conservation Biology **1(1)**:59–62.

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

Hudson, P. J. 1986. The effect of a parasitic nematode on the breeding production of Red Grouse. Journal of Animal Ecology **55**:85–92.

Jacobson, E. R., and J. M. Gaskin. 1990. Clinicopathologic investigations on an upper respiratory disease of free-ranging desert tortoises, *Xerobates agassizii.* U.S. Contract report. Bureau of Land Management, Department of the Interior, Riverside, California.

Jenkins, C. D., S. A. Temple, C. van Riper, and W. R. Hansen. 1989. Disease-related aspects of conserving the endangered Hawaiian Crow. Pages 77–87 in J. E. Cooper, editor. Disease and threatened birds. Technical publication No. 10. Cambridge, England.

Kear, J., and P. Palmes. 1980. Andean and James Flamingos. International Zoo Yearbook **20**:17–23.

Kennedy-Stoskopf, S. 1989. Infectious diseases: Cause or effects? Journal of Zoo and Wildlife Medicine **20(3)**:247–248.

Kepler, C. B. 1978. Captive propagation of Whooping Cranes: A behavioral approach. Pages 231–241 in S. A. Temple, editor. Endangered birds: Management techniques for preserving threatened species. University of Wisconsin Press, Madison, Wisconsin.

Lacy, R. C. 1987. Loss of genetic diversity from managed populations: Interacting effects of drift, mutation, immigration, selection, and population subdivision. Conservation Biology **1(2)**:143–158.

Lacy, R. C., N. R. Flesness, and U. S. Seal. 1989. Puerto Rican Parrot (*Amazona vittata*) population viability analysis and recommendations. Captive Breeding Specialist Group, Apple Valley, Minnesota.

Linz, G. M., J. E. Davis, Jr., R. M. Engeman, D. L. Otis, and M. L. Avery. 1991. Estimating survival of bird carcasses in cattail marshes. Wildlife Society Bulletin **19**:195–199.

Luthin, C. S., G. W. Archibald, L. Hartman, C. M. Mirande, and S. Swengel. 1985. Captive breeding of endangered cranes, storks, ibises, and spoonbills. International Zoo Yearbook **24/25**:25–39.

Mann, P. C., M. Bush, M. J. G. Appel, B. A. Beehler, and R. J. Montali, 1980. Canine parvovirus infection in South American canids. Journal of the American Veterinary Medical Association **177**:779–783.

May, R. M. 1988. Conservation and disease. Conservation Biology **2(1)**:28–30.

Montali, R. J., M. Bush, and G. A. Greenwell. 1976*a.* An epornitic of duck viral enteritis in a zoological park. Journal of the American Veterinary Medical Association **169(9)**:954–958.

Montali, R. J., M. Bush, C. O. Thoen, and E. Smith. 1976*b.* Tuberculosis in captive exotic birds. Journal of the American Veterinary Medical Association **169(9)**:920–927.

Montali, R. J. M. Bush, and E. E. Smith. 1978. Pathology of tuberculosis in captive exotic birds. Pages 209–215 in Proceedings: Mycobacterial infections of zoo animals symposium. Smithsonian Institution Press, Washington, D.C.

Murphy, D. D., K. E. Freas, and S. B. Weiss. 1990. An environment-metapopulation approach to population viability analysis for a threatened invertebrate. Conservation Biology **4(1)**:41–51.

Nettles, V. F., J. H. Shadduck, R. K. Sikes, and C. R. Reyes. 1979. Rabies in translocated raccoons. AJPH **69(6)**:601–602.

O'Brien, S. J., M. E. Roelke, L. Marker, A. Newman, C. A. Winkler, D. Meltzer, L. Colly, J. F. Evermann, M. Bush, and D. E. Wildt. 1985. Genetic basis for species vulnerability in the cheetah. Science **227**:1428–1434.

Quinn, J. F., and A. Hastings. 1987. Extinction in subdivided habitats. Conservation Biology **1(3)**:198–208.

Reece, R. L. 1989. Avian pathogens: Their biology and methods of spread. Pages 1–23 in J. E. Cooper, editor. Disease and threatened birds. Technical publication No. 10. , Cambridge, England.

Ritchie, B. W., F. D. Niagro, P. D. Lukert, K. S. Latimer, W. L. Steffens, and N. Pritchard. 1989. A review of psittacine beak and feather disease. Journal of the Association of Avian Veterinarians **3(3)**:143–148.

Saumier, M. D., M. E. Rau, and D. M. Bird. 1986. The effect of *Trichinella pseudospiralis* infection on the reproductive success of captive American Kestrels (*Falco sparverius*). Canadian Journal of Zoology **64**:2123–2125.

Scott, M. E. 1988. The impact of infection and disease on animal populations: Implications for conservation biology. Conservation Biology **2(1)**:40–56.

Seal, U. S., and R. C. Lacy. 1989. Florida panther (*Felis concolor coryi*) viability analysis and species survival plan. Captive Breeding Specialist Group, Apple Valley, Minnesota.

Shaffer, M. L. 1985. The metapopulation and species conservation: The special case of the Northern Spotted Owl. Pages 86–99 in R. J. Gutierrez and A. B. Carey, editors. Ecology and management of the Spotted Owl in the Pacific Northwest. General technical report PNW-185. U.S. Department of Agriculture–Forest Service,

Shaffer, M. L. 1990. Population viability analysis. Conservation Biology **4(1)**:39–40.

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(3)**: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. Thilsted, B. Burgess, and M. Richard. 1985. Pigeon herpesvirus mortalities in foster reared Mauritius Pink Pigeons. Pages 69–70 in Proceedings of the American Association of Zoo Veterinarians.

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, California.

Thorne, E. T., and E. S. Williams. 1988. Disease and endangered species: The black-footed ferret as a recent example. Conservation Biology **2(1)**:66–74.

U.S. Fish and Wildlife Service. 1987. Recovery plan for the Puerto Rican Parrot, *Amazona vittata.* U.S. Fish and Wildlife Service, Atlanta, Georgia.

van Riper, C., S. G. van Riper, M. L. Goff, and M. Laird. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. Ecological Monographs **56**:327–344.

Watkins, D. L., N. L. Letvin, A. L. Hughes, and T. F. Fedder. 1990. Molecular cloning of cDNAs that encode MHC class I molecules from a New World primate (*Saguinus oedipus*): Natural selection acts at positions that may affect peptide presentation to T cells. Journal of Immunology **144**:1136–1143.

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.