Abstract: The recent review by Caughley (1994) on approaches used in conservation biology suggested that there are two: the small population paradigm and the declining population paradigm. We believe that this division is overly simplistic and that it should not be perpetuated. Both the deterministic factors that reduce population size and the stochastic factors that lead to the final extinction of a small population are critical to consider in preventing extinction. Only through an overall and comprehensive effort, which we call inclusive population viability analysis, can extinction processes be understood and mitigated. In this context we discuss Caughley's comments about genetics, demography, and general population viability, with particular attention to cheetahs (*Acinonyx jubatus*) and Pacific salmon (*Oncorhynchus* sp.).

Directions in Conservation Biology: Comments on Caughley

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Abstract: *The recent review by Caughley (1994) on approaches used in conservation biology suggested that there are two: the small population paradigm and the declining population paradigm. We believe that this division is overly simplistic and that it should not be perpetuated. Both the deterministic factors that reduce population size and the stochastic factors that lead to the final extinction of a small population are critical to consider in preventing extinction. Only through an overall and comprehensive effort, which we call inclusive population viability analysis, can extinction processes be understood and mitigated. In this context we discuss Caughley's comments about genetics. demography. and general population viability, with particular attention to cheetahs* (Acinonyx jubatus) *and Pacific salmon* (Oncorhynchus sp.).

Direcciones en la biología de la conservación: Comentarios sobre Caughley

Resumen: *La revisión reciente hecha por Caughley (1994) sobre aproximaciones en la biología de la conservación sugiere que existen dos de ellas: El paradigma de la población pequeña y el paradigma de la población en disminución. Sentimos que esta división es demasiado simplista y no debería ser perpetuada. Tanto los factores determinísticos que reducen el tamaño poblacional, como los factores estocásticos que conducen a la extinción de una población pequeña son críticos en la prevención de su extinción. Únicamente a través de un esfuerzo general y comprensivo. que incluso llamaríamos análisis de viabilidad poblacional. se podrán entender los procesos de extinción y ser mitigados. En éste contexto, discutimos los comentarios hechos por Caughley sobre genética. demografía y viabilidad poblacional general con particular atención en los chitas* (Acinonyx jubatus) *y el salmón del Pacífico* (Oncorhynchus sp.)

Introduction

Just before he died, Caughley (1994) wrote a provocative review outlining his perspective of the scientific approaches used in conservation biology (see also Caughley & Gunn 1995). His essay, as probably intended, has generated substantial controversy and resulted in the questioning of some of the tenets presently used in conservation biology research. Although it is useful to evaluate the accomplishments and problems in a discipline,

we feel that Caughley constructed a false dichotomy between what he calls the "small population paradigm" and the "declining population paradigm." His review also contained a number of misunderstandings about the application of ideas from the demography and genetics of small populations to conservation biology. This potentially divisive separation of approaches unfortunately comes when a number of new molecular genetic techniques promise exciting and detailed understanding of the genetics and evolution of populations and species and when new, spatially-explicit computer models promise greater understanding of habitat fragmentation and metapopulation dynamics.

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An arbitrary separation of approaches as delineated by Caughley may unprofitably polarize conservation biologists and result in pitting different approaches against each other when hostile political forces are attempting to discredit many conservation efforts. Contrary to Caughley's view, it appears to us that in recent years there has been greater emphasis on and more success in integrating natural-history information for particular endangered species into a general theoretical context, an effort that appears to he supported by both the more applied and the more theoretical conservation biologists. For example, efforts in this direction have been made by the Conservation Breeding Specialist Group of The World Conservation Union (IUCN) to include habitat considerations into their population viability analyses. We applaud the successes of the scientific approaches described by Caughley in identifying the factors causing population or species declines, and we urge their general application, a tradition in conservation biology (Myers 1987). We recognize that it is critical to identify and mitigate the factors in the decline of a species (Long et al, 1995). As conservation biologists, we should always remember that our motivation is not to win a debate or to demonstrate the correctness of a given approach hut to use all methods at our disposal to maintain the integrity of natural ecosystems and stem the loss of biodiversity.

We discuss some more conclusions of Caughley (1994), and we give what we hope is a constructive perspective on his commentary We then discuss Pacific salmon, (*Oncorbynchus* sp.) a species tit could have benefited greatly from the integration of Caughley's polar paradigms, and the cheetah, (*Acinonyx jubatus*) genetic studies of which have been a main subject of recent criticism, including that of Caughley. Finally. we discuss a melding of the paradigms into an "inclusive population viability analysis" and try to encourage a profitable synergism among conservation biologists with different viewpoints, as Caughley himself was apparently attempting.

(...maybe he was arguing for a shift in resources,
Δ in focus

Perspective

Caughley (1994) suggested that there are two basic approaches to understanding the factors influencing extinction. First, he suggested that the small-population paradigm endeavors to determine "the effects of smallness on the persistence of a population" and deals with "the risk of extinction inherent in low numbers." Second, he states that the declining population paradigm deals with "the cause of smallness and its cure" and "with processes by which populations become extinct." As he summarizes, the factors causing extinction under the small-population paradigm are environmental stochasticity and catastrophes, demographic stochasticity, and genetic deterioration (Frankel & Soulé 1981; Shaffer

1981 1987; Lande 1988a; Lande 1993), whereas under the declining population paradigm the factors causing extinction are overkill. habitat destruction and fragmentation, impact of introduced species, and chains of extinction (Diamond 1984, 1989).

We believe that this separation is artificial. In general. the factors under the small-population paradigm are the stochastic ones that may result in the proximate cause of extinction, and the ones under the declining population paradigm are the deterministic (or ultimate) ones that reduce the population size so that it becomes vulnerable to random events and phenomena. As suggested by Shaffer (1981), the concern over stochastic factors arose precisely because of the realization that, even with adequate natural habitat and species protection. and even with a positive mean population growth rate, random factors may cause a species with low numbers to become more vulnerable or extinct. Researchers attempting to understand the proximate causes of extinction have always known that without removal of the deterministic driving forces, such as loss of habitat, introduced predators, and pollution, the population or species will inevitably go extinct. *why so much attn to prox causes. then?*

Further, once deterministic factors have led to small, fragmented, and isolated populations, stochastic factors may further reduce numbers. and the interaction of forces may contribute to further endangerment, as illustrated by the extinction vortices of Gilpin and Soulé (1986). We think it more productive and accurate to cast the discussion in terms of an analysis of viability that considers both the generally anthropogenic ultimate causes and the stochastic proximate causes—an inclusive population viability analysis. We consider characteristics of population viability analysis (PVA) that are crucial to this inclusive approach.

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Genetic Factors

Caughley (1994) acknowledged that genetic considerations in avoiding inbreeding and maximizing retention of genetic variation have played a major role in captive breeding. Insufficient attention to small-population threats has resulted in damaging losses of viability and fecundity in many—now inbred—captive stocks (Ralls & Ballou 1983: Ralls et al. 1988: Lacy et al. 1993). Prior to the work of Ralls and Ballou, zoo curators rarely acknowledged that inbreeding might contribute to the rapid deterioration in vigor and fitness of small. captive groups.

In addition, genetics has made an important contribution to understanding threats facing natural populations. Loss of genetic diversity in small populations has apparently reduced fitness in natural populations of plants (Bijlsma et al. 1994), topminnows (*Poeciliopsis occidentalis*; Vrijenhoek 1994), wolves (*Canis lupus*; Wayne et al. 1991), African lions (*Panthera leo*; Packer et al. 1991),

and Florida panthers (*Fells concolor coryi*: Roelke et al. 1993). But perhaps the most important contributions of genetic information to conservation have been its general utility in the identification of species, understanding the structure and differentiation of populations, describing the mating or reproductive system, or determining other evolutionary, ecological, or behavioral information unrelated to selective differences.

Demographic Factors and Stochasticity

Small-population models have also forced us to reexamine some of the methodologies of demographic analysis that are well entrenched in wildlife ecology and management. For example, standard life-table analyses on long-term average birth and death rates will systematically underestimate the rates of population decline when vital rates vary over time or space (Tuljapurkar & Orzak 1980; Goodman 1987; Beissinger 1995). Caughley identifies the use of maximum-sustained-yield models to prevent extinction by overkill as one of the "areas of theory to which the declining-population paradigm can lay claim." But harvesting strategies based on models that neglect the possibility of extinction have been found to provide lower mean annual yields and to subject populations to greater risk. of extinction than do optimal harvesting strategies that take into consideration that demographic and environmental stochasticity can lead to extinction (Lande et al. 1995). Thus. determination of optimal harvesting strategies that do not jeopardize both yield and population persistence requires the joint application of declining-population and small-population theories. Similarly, the risk that economic weighing of the value of a sustained resource against the discount rate will lead to deliberate harvest to extinction is altered by the inclusion of stochastic processes in the models (Lande et al. 1994). That stochastic processes by themselves, or in interaction with deterministic factors, are of more than theoretical interest is demonstrated by the collapse of many managed fisheries (Ludwig et al. 1993), the loss to disease of the last wild population of black-footed ferrets (*Mustela nigripes:* Clark 1989; Seal et al. 1989). and the decimation and subsequent extirpation of the last nonmigratory population of whooping cranes (*Grus americana*) as a result of a hurricane (Doughty 1989).

Synthesis of Factors in a PVA Approach

Caughley suggests that the strengths of small-population models include their theoretical underpinnings and potential for generality across species;. We agree that these are positive and appealing aspects that have allowed testing of the underlying hypotheses of these models and resulted in both extensive investigation of its theo-

retical constructs and experimental examination of them. Further, small-population models may be attractive because the theory can be mathematically elegant (or at least mathematically well-defined). But models are important for more than their aesthetic qualities. For decades there has been discussion about declining populations, but without models or theory that would allow precise description or prediction. A strong advantage of many of the small-population models is that they can be subjected to testing by examination of the properties of the models and assumptions (Taylor 1995), by comparison of the fit of the model results to data on past population dynamics (Mirande et al. 1991), and by comparison of predictions for the future to monitored performance. In addition, they can he used to determine what other population information is necessary to predict population *trends more* accurately.

Substantial experimental research has been conducted to determine the general validity of small-population models. Laboratory research has generally supported its genetic assumptions (Frankham 1995) and has further demonstrated, for example, that all fitness components can he influenced by inbreeding (Miller & Hedrick 1993), that inbreeding depression may by somewhat greater in stressful environments (Dudash 1990: Wolfe 1993; Miller 1994) and that inbreeding may result in lowered fitness in natural environments (Jiménez et al. 1994; Keller et al. 1994). This is not to say that there are no unresolved issues. such as the impact of bottlenecks on genetic variation and the association of genetic variation, fitness. and extinction (Hedrick & Miller 1992).

The Florida panther is a case that exemplifies how the quantitative nature of small-population models helps drive analysis of data, which in mm provides guidance co conservation efforts. Intensive field research provided a record of most of the deaths that occurred during the past decade. Yet there had not been a detailed examination of the mean mortality rate and the variation in mortality across years. until such was required by the application of PVA models to conservation planning. Analysis of the data and population projections with PVA modeling revealed that the panthers are extremely vulnerable to small-population problems. such as inbreeding and an absence of mates for some animals because of the locally variable sex ratios of breeders Accordingly, conservation efforts for Florida panthers now include the restoration of genetic variation and supplementation of the breeding population through augmentation from the Texas population of the species (Seal 1992,1994; Hedrick 1995).

In the case of the Whooping Crane, even more-detailed data on mortality and reproduction were available: a tally of recruitment and deaths had been recorded every year since 1938. A PVA built upon the earlier deterministic models of population growth (Binkley & Miller 1983; Boyce 1987) and incorporated stochastic processes that could destabilize even a growing population

(Mirande et al. 1991). When applied to the population status as it existed in 1938, the PVA model accurately projected population growth and the magnitude of fluctuations over the subsequent 52 years. The analyses indicated that Whooping Cranes are now at large enough numbers that the threats of inbreeding and demographic stochasticity are declining; the primary threat remaining is the possibility of local catastrophic loss of the sole remaining population due to disease or other factors (Mirande et al. 1991). This risk, which could not have been evaluated in a wholly deterministic analysis, is being addressed through the establishment of a nonmigratory population of Whooping Cranes i" Florida.

The interaction of demographic and environmental factors also affects small populations. For example, the last five Dusky Seaside Sparrows (*Ammodrumus maritimus nigrescens*) were males, a" improbable, stochastic event that effectively terminated the taxon. Similarly, the last Illinois population of lakeside daisy (*Hymenoxys acaulis* var. *glabra*) was all of the same self-incompatible mating type (DeMauro 1993). Rare plants (Karron 1987) and those in small populations (Widen 1993) can suffer reduced seed set due to lack of pollinators. Other vital rates are also affected by stochastic processes acting on local populations of plants (Schemske et al. 1994). Small, local populations of animals have been found to be more likely to go extinct (Soulé et al. 1988; Berger 1990; Rosenzweig & Clark 199-i; Hanski et al. 1995; Newmark 1995). An unusually dry year in a Costa Rica" cloud forest apparently caused the extinction of the golden toad (*Bufo periglenes*) and the local extirpation of the harlequin frog (*Atelopus varius*) (Pounds & Crump 1994).

Caughley suggests that consideration of the effects of small populations has not significantly contributed to preventing extinctions. Given the high profile of rhe Spotted Owl (*Strix occidentalis caurina*) *controversy* (see Harrison et al. 1993 and references therein), it is hard to understand Caughley's statement that he "can find no example of the idea of minimum viable population size being applied" to species conservation. Further, several studies have demonstrated that excessive emphasis on the obvious deterministic factors can be misleading, resulting in conclusions that are too optimistic about viability and persistence. For example, it was generally accepted for many years that predation by Common Ravens (*Corvus corax*) on young desert tortoises (*Gopherus agassizii*) was the major factor jeopardizing their survival in some parts of the southwest. A PVA showed, however, that the most sensitive stage by far were mature females, and an emphasis on reducing raven predation erred in mistaking a highly visible impact for a demographically significant one (Doak et al. 1994). Work on loggerhead sea turtles (*Caretta caretta*) has similarly shown the difficulty in guessing the relative significance of different vital rates in determining popu-

lation growth (Crouse et al. 1987). Thus, one cannot always interpret the significance of deterministic factors unless a proper inclusive PVA is carried out.

Caughley further states that no "instance of extinction by genetic malfunction has been reported." Although the strength of the evidence can he disputed, several studies have reported extinctions caused—in the end—by "genetic malfunctions" (e.g., Heath Hens [*Tympanchus cupido cupido*; Simberloff 1988] and the Swedish population of Middle Spotted Woodpeckers [*Dendrocapus medius*; Pettersson 1985]. More important, Caughley's assertion illustrates a basic misunderstanding of the impact of genetics on extinction. Genetics does not operate in isolation but will influence a population through its effects on disease resistance, viability, reproductive success, behavior, physiology, and other characteristics. For example, in zoo animals inbred individuals often die from a variety of *medical* problems, whereas mortality in outbred animals is more likely from accidents (Ralls et al. 1980).

Disagreement over whether or "or genetics should be considered in demographic predictions of population persistence has been unfortunate and misleading. Extinction is a demographic process that *is* likely to be influenced by genetic effects under some circumstances. The important issue is to determine under what conditions genetic concerns are likely to influence population persistence (Nunney & Campbell 1993; Mills & Smouse 1994). For example, lethal or eve" sublethal alleles may be purged in small populations, but slightly deleterious variants may become fixed and thereby lower viability and mating success (Hedrick 199-i). Lande (1988a), who emphasized the importance of demographic factors over genetic ones in causing extinction, has recently suggested (Lande 1995) that the population size necessary to maintain genetic variation is an order of magnitude higher than previously thought, which places greater emphasis on genetic factors. Further, recent theoretical work suggests that the fixation of new mutants with slightly detrimental effects may lead to a long-term decline in population fitness and to eventual extinction (Lynch et al. 1995).

Perhaps most important, we need to recognize when management recommendations based upon strictly demographic or genetic considerations may actually conflict with each other. For example, Ryman and Laikre (1991) have considered supportive breeding in which a portion of wild parents are brought into captivity for reproduction and their offspring are released into the natural habitat, where they mix with wild conspecifics. Programs similar to this are carried out in a number of species to increase population size and thereby temper stochastic demographic effects. But under some circumstances, supportive breeding may reduce effective population size and cause a drastic reduction in genetic variation (Ryman & Laikre 1991; Ryman et al. 1995; but see Hedrick et al. 1995).

Case Studies

There are number of species for which small population considerations are of great significance. We discuss cheetahs, because of the detailed commentary by Caughley, and Pacific salmon, because of the special relevance of small-population theory to their survival.

Cheetah

The conservation biology history of the cheetah developed by O'Brien (O'Brien et al. 1983, 1985) has been the focus of extensive recent controversy among Caughley (199-i) and others (Car" & Laurenson 1994; Merola 199-t). We discuss it to point out the misrepresentations and misinterpretations of these data. Although we do not completely agree with Caughley, we believe that a more balanced evaluation of these data based on evolutionary genetics is necessary to achieve a more integrated assessment of the cheetah's vulnerability.

The examination of molecular genetic variation in the cheetah is probably the most extensive of any endangered species and includes estimates of variation in allozymes, soluble proteins, major histocompatibility genes (from both restriction fragment length polymorphisms [RFLPs] and tissue transplants), mitochondrial DNA, minisatellites, and microsatellites. For allozymes in particular. the extent of variation is low in cheetahs, whereas for mtDNA, minisatellites. and microsatellites, the extent of variation is nearly as high as in other big cats (Menotti-Raymond & O'Brien 1993, 1995). The initial findings of low allozyme variation in the cheetah led to the conclusion that the cheetah is vulnerable to extinction because of its lack of genetic variation. But the equilibrium genetic variation among species is expected to vary. largely because of differences in long-term effective population size. A species with low genetic variation does not necessarily suffer a decrease in fitness. Caughley provides a brief discussion of why a simple relationship between heterozygosity and vulnerability to extinction is unlikely (see also Hrdrick et al. 1986).

On the other hand, low genetic variation in a species may be indicative of a recent population bottleneck, and there are several reasons to expect that such a bottleneck does potentially indicate vulnerability to extinction. First, a recent bottleneck may indicate demographic instability that is not obvious from contemporary population size alone. Second, a species that has gone through a bottleneck severe enough to erode detectable molecular genetic variation may suffer from fixation of detrimental alleles with the consequent lowered fitness that may increase vulnerability to extinction. Finally, loss of genetic variation caused by the bottleneck may limit the ability of the population to evolve and adapt. The more recent a bottleneck has been, the more we would expect the bottleneck to influence the future of a species.

The low allozyme variation in cheetahs may actually indicate past history. either because of one or more bottlenecks or because of a chronically low effective population size due to. for example, metapopulation dynamics (Gilpin 1991; Hedrick 1996). The higher variation for mtDNA, minisatellites. and microsatellites may also be expected because of the higher mutation rates for these genes (Menotti-Raymond & O'Brien 1993, 1995). In fact. these molecular methods and others available today (Smith & Wayne 1996) may eventually allow us to gain some understanding of the previous history of cheetahs (Hedrick 1996). There does appear to be variation in genes influencing fitness. because evidence of inbreeding depression exists for cheetahs (Hedrick 1987; Caughley 1994; Wielebrowski 1996). Because the rate of mutation for quantitative traits per genome is thought to be of similar magnitude to the rates of mutation for minisatellites and microsatellites. variation in fitness traits is not unexpected even in the absence of variation in allozyme loci (see discussion in Hedrick 1996; Soulé & Zegers 1996).

Overall, the molecular genetic information on the cheetah may well provide insight into its population biology, but the problems related to its numbers in the wild are probably multifold and not entirely understood. As discussed by Caro and Laurenson (1994), the main source of mortality in wild cheetahs appears to be killing by lions (*Panthera leo*). but changes in the habitat by humans also appear to have had negative consequences. Furthermore. cheetahs in southern Africa, which appear to have somewhat loner genetic variation than those in eastern Africa, ~~are much higher in densi~~ and are less endangered. Even in captivity. diet. husbandry, and understanding of mating behavior appear to be of greater significance than genetic considerations to successful breeding and maintenance. It is important to recognize. however. that it is often not possible or meaningful to attribute birth and deaths to purely genetic or nongenetic causes. For example. greater predation could be related to inbreeding depression. *No ~ predictions of great chance*

What began as a possible case of genetic vulnerability has lately become a more complicated story involving issues of husbandry. predation. and habitat modification. The history of the cheetah in conservation biology may eventually be of use because it urges caution when few of the facts are known. Obviously. it behooves conservation biologists who wish to use genetics in endangered species studies to carefully qualify the implications of their findings and not to overemphasize their significance. If not. as in the cheetah story. genetic information may be discarded. rightly or wrongly, when it may be of real value.

Pacific Salmon

'The current crisis in the conservation of Pacific salmon has been caused to some extent by the lack of applica-

tion of small-population thinking to the management of wild salmon. Serious declines in salmon from the Columbia River, much of it caused by deterministic factors such as hydroelectric development, have been recognized for over 100 years (Allendorf & Waples 1995). One response was a large system of hatcheries and other programs specifically designed to offset losses from hydroelectric development. Beyond these programs, salmon management has responded to these declines largely through the regulation of fisheries based upon the principles of stock-recruitment and maximum sustained yield (Ricker 1754; Beverton & Holt 1957). Fishery managers have attempted to maximize surplus production (i.e., fish available for the catch) by maintaining the number of spawners at an abundance at which, according to stock-recruitment theory, they are likely to be most productive.

It has long been recognized that the fundamental unit of replacement of recruitment for anadromous (migratory) salmonids is the local population because of its homing behavior (Rich 1939; Ricker 1972). An adequate number of individuals in each of the small, local reproductive populations is needed to ensure persistence in the face of demographic, environmental, and genetic uncertainty. The homing of salmon i" their natal streams produces a network of local reproductive populations that are distinct and adapted i" specific environmental conditions. Groups of local salmon populations may function as metapopulations on a short time scale, and on an evolutionary time scale, most salmon populations are probably connected by migration, straying, or recolonization from other populations. Such connectedness may homogenize neutral genetic markers to some extent over local populations, but adaptive differences may remain in spits of gene flow.

The distinction between the fished stock and the local reproductive population is critical (Beverton et al. 198-i). In practice, it has been extremely difficult to regulate losses on the basis of individual local populations. Thousands of local populations make up the West Coast salmon fishery, and many of these are likely to be intermingled in any particular catch. The result of regulating fishing on a stock basis and ignoring the reproductive units that together constitute a stock has been the disappearance or extirpation of many local populations (Clark 1984).

Caughley recommends that extirpated populations be replaced by restocking through translocation. This recommendation ignores the potential importance of genetically based local adaptations. Attempted translocation within the range of Pacific salmon have generally not been successful, in either North America (Withler 1982) or Asia (Altukhov & Salmenkova 1987). For example, efforts to reintroduce sockeye salmon (*Oncorhynchus nerka*) into appropriate habitat in the Fraser River system generally have failed. This has been particularly true

of efforts to introduce lower-river stocks into upriver areas. Sockeye salmon from the lower Fraser River apparently lack the genetic (physiological) capacity to store energy reserves sufficient for the long migration into upriver areas that were depleted after a rock slide impeded upstream migration early in this century (Foerster 1968).

In addition, Riddell (1993) detailed an example from the Adams River, a tributary of the Fraser River. A logging dam built in 1908 blocked access of sockeye salmon to the upper Adams River from 1708 to 1921; these runs had been among the largest sockeye runs in the Fraser River system. This area has 1.2 million m^2 of spawning area, which should be sufficient to support 6 million adult sockeye per year based on productivity of other sockeye populations in the area. Sixteen attempts between 1949 and 1975 to reintroduce sockeye to these spawning areas were not successful in reestablishing the run. Today, only a few fish return to spawn in the upper Adams River.

Such observations provide strong evidence that many spawning populations of anadromous salmonids exhibit highly specific local adaptations for a number of different traits. These adaptations are likely to be the result of genetic differences between local populations at many loci. On this basis we expect it to be difficult to "replace" a local population with transplants from non-local populations. Only by understanding that the fundamental unit in salmon is the local population, and not the ocean stock, are these complexities apparent. Of course, one should not assume that other species besides salmon necessarily have specific adaptations unless they are demonstrated direct& or suggested by genetic evidence, particularly when the per-generation migration is large. Even in salmon successful transplants of the nonanadromous kokonee are quite common.

Melding of the Paradigms

Caughley ends his essay on a positive point and suggests that "each paradigm has much to learn from the other and in combination they might enlarge our idea of what is possible." He gives several examples that illustrate situations in which both approaches contribute to preventing extinctions. The prime example is the Lord Howe Woodhen (*Tricholimnas Sylvestris* (Sclater)) for which introduced feral pigs (*Sus scrofa*) were identified through various experiments as the ultimate cause of the decline of the population. While this identification was taking place, the remaining birds were in a captive breeding program (this program was designed primarily to produce more woodhens before extinction [Miller & Mullette 1985] and did consider maintenance of genetic variation and avoidance of inbreeding). A second example is the interaction of metapopulation dynamics and habitat fragmentation as a cause of extinction. For exam-

ple, the revision of timber-harvest practices to accommodate (partly) the Northern Spotted Owl was the result of PVAs that revealed that changes in the distribution of habitat across the landscape can, through local population processes, cause extinction (Lande 1988b). Contrary to Caughley's assertion that PVA ignores external influences on population's rate of increase, it is an excellent tool for integrating deterministic and stochastic factors. What PVA models bring to the analysis of wildlife populations is the consideration of stochastic processes, but they do not leave out the deterministic threats of habitat loss and alteration, over-harvest, and the impact of exotics.

The different approaches discussed by Caughley have much in common because they both focus on the fate of a given species. As suggested by Caughley and supported by us, a broader understanding of the factors influencing endangerment and extinction, based on an inclusive approach to PVA should be our goal.

Acknowledgments

Literature Cited

Allendorf, F. W., and R. S. Waples. 1995. Conservation genetics of salmonid fishes. Pages 238–280 in J. C. Avise and J. L. Hamrick, editors. Conservation genetics. Chapman and Hall, New York.

Altukhov Y. P., and E. A. Salmenkova. 1987. Stock transfer relative to natural organization. management, and conservation of fish populations. Pages 333–344 in N. Ryman and F. Utter, editors. Population genetics and fishery management. University of Washington Press, Seattle. Washington.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. U. K. Min. Agricv. Fish., Fish. Invest. (Ser. 2) 19.

Beverton, R. J. H., et al. 1984. Dynamics of single species: group report. Pages 13–58 in R. M. May. editor. Dahlem Koknferenzen. Springer-Verlag. Berlin.

Beissinger, S. R. 1995. Modeling extinction in periodic environments: Everglades water levels and snail Kite population viability. Ecological Applications 5:618–631.

Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. Conservation Biology 4:91–98.

Bijlsma, R., N. J. Ouborg, and R. van Treuren. 1994. On genetic erosion and population extinction in plants: a case study in Scabiosa columbaria and Salvia pratensis. Pages 255–271 in V. Loescheke, J. Tomiuk, and S. K. Jain, editors. Conservation genetics. Birkhäuser Verlag, Basel, Switzerland.

Binkley, C. S., and R. S. Miller. 1983. Population characteristics of the Whooping Crane, Grus americana. Canadian Journal of Zoology 61:2768–2776.

Boyce, M. S. 1987. Time-series analyses and forecasting of the Aransas Wood Buffalo Whooping Crane population. Pages 1–9 in J. C. Lewis and J. W. Ziewitz, editors. Proceedings of the 1985 crane workshop. Platte River Whooping Crane Habitat Maintenance Trust and U.S. Fish and Wildlife Service. Grand Island, Nebraska.

Caro, T. M., and M. K. Laurenson. 1994. Ecological and genetic factors in conservation: a cautionary tale. Science 263:485–486.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Caughley, G., and A. Gunn. 1995. Conservation biology in theory and practice. Blackwell Science, Cambridge, Massachusetts.

Clark, C. W. 1984. Strategies for multispecies management: objectives and constraints. Pages 303–312 in R. M. May. editor. Dahlem Konferenzen. Springer-Verlag, Berlin.

Clark, T. W. 1989. Conservation biology of the black-footed ferret. Wildlife Preservation Trust International, Philadelphia.

Crouse, D., Crowder. L., and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423.

DeMauro, M. M. 1993. Relationship of breeding system to rarity in the lakeside daisy (Hymenoxys acaulis var. glabra). Conservation Biology 7:542–550.

Diamond, J. M. 1984. "Normal" extinction of isolated populations. Pages 191–246 in M. H. Nitecki. editor. Extinctions. Chicago University Press, Chicago.

Diamond, M. M. 1989. Overview of recent extinctions. Pages 376–341 in D. Western and M. Pearl. editors. Conservation for the twenty-first century. Oxford University Press, New York.

Doak D. F., P. Kareiva. and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the Mojave Desert. Ecological Applications 4:446–460.

Doughty, R. W. 1989. Return of the Whooping Crane. University of Texas Press, Austin.

Dudash, M. R. 1990. Relative fitness of selfed and outcrossed progeny in a self-compatible protandrous species, Sabatia angularis L (Gentianaceae): a comparison in three environments. Evolution 44: 1129–1139.

Foerster, R. E. 1968. The sockeye salmon. Bulletin 162. Fisheries Research Board of Canada.

Frankel, O. H., and M. E. Soulé. 1981. Conservation and evolution. Cambridge University Press, Cambridge. United Kingdom.

Frankham, R. 1995. Conservation genetics. Annual Reviews of Genetics 29:305–327.

Gilpin, M. E. 1991. The genetic effective size of a metapopulation. Biological Journal of Linnean Society 42:165–175.

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

Goodman, D. 1987. The demography of chance extinction. Pages 11–34 in M. Soulé. editor. Viable populations for conservation. Cambridge University Press. Cambridge, United Kingdom.

Hanski, I., J. Poyry, T. Pakkala, and M. Kussaari. 1995. Multiple equilibria in metapopulation dynamics. Nature 377:618–621.

Harrison, S., A. Stahl, and D. Doak. 1993. Spatial models and spotted owls: exploring some biological issues behind recent events. Conservation Biology 7:950–953.

Hedrick, P. W., P. F. Brussard, F. W. Allendorf, J. A. Beardmore, and S. Orzack. 1986. Protein variation. fitness, and captive propagation. Zoo Biology 5:91–99.

Hedrick, P. W. 1987. Genetic bottlenecks. Science 237:963.

Hedrick, P. W., and P. S. Miller. 1992. Conservation genetics: techniques and fundamentals. Ecological Applications 2:30–46.

Hedrick, P. W. 1994. Purging inbreeding depression and the probability of extinction: full-sib mating. Heredity 73:363–372.

Hedrick, P. W. 1995. Gene flow and genetic restoration: the Florida panther as a case study. Conservation Biology 9:996–1007.

Hedrick, P. W. 1996. Bottleneck(s) or metapopulation in cheetahs? Conservation Biology 10:897–899.

Hedrick, P. W., D. Hedgecock, and S. Hammelberg. 1995. Effective population size in winter-run chinook salmon. Conservation Biology 9:615–624.

Jimenez, J. A., K. A. Hughes, G. Alaks, L. Graham, and R. C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. Science 265:271–274.

Karron, J. D. 1987. The pollination ecology of co-occurring geographically restricted and widespread species of Astragalus (Fabaceae). Biological Conservation 39:179–193.

Keller, L. F., P. Arcese, J. N. M. Smith, W. M. Hochachka, and S. C. Stearns. 1994. Selection against inbred song sparrows during a natural population bottleneck. Nature 372:356–357.

Lacy, R. C., A. M. Petric, and M. Warneke. 1993. Inbreeding and outbreeding depression in captive populations of wild species. Pages 352–374 in N. W. Thornhill, editor. The natural history of inbreeding and outbreeding. University of Chicago Press, Chicago.

Lande, R. 1988a. Genetics and demography in biological conservation. Science 241:1455–1450.

Lande, R. 1988b. Demographic models of the Northern Spotted Owl. Oecologia 75:601–607.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity, and random catastrophes. American Naturalist 142:911–927.

Lande, R. 1995. Mutation and conservation. Conservation Biology 9: 782–791.

Lande, R., S. Engen, and B.-E. Saether. 1994. Optimal harvesting, economic discounting and extinction risk in fluctuating populations. Nature 372:88–90.

Lande, R., S. Engen, and B.-E. Saether. 1995. Optimal harvesting of fluctuating populations with a risk of extinction. American Naturalist 145:728–745.

Long, L., L. Saylor, and M. E. Soulé. 1995. A pH/UV-B synergism in amphibians. Conservation Biology 9:1301–1303.

Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation and conservation: lessons from history. Science 260:17–36.

Lynch, M., J. Conery, and R. Burger. 1995. Mutational meltdown in sexual populations. Evolution 49:1067–1080.

Menotti-Raymond, M., and S. J. O'Brien. 1993. Dating the genetic bottleneck of the African cheetah. Proceedings of the National Academy of Sciences USA 90:3172–3176.

Menotti-Raymond, M., and S. J. O'Brien. 1995. Evolutionary conservation of ten microsatellite loci in four species of Felidae. Journal of Heredity 86:319–322.

Merola, M. 1994. A reassessment of homozygosity and the case for inbreeding depression in the cheetah, Acinonyx jubatus: implications for conservation. Conservation Biology 8:961–971.

Miller, B., and K. J. Mullete. 1985. Rehabilitation of an endangered Australian bird: the Lord Howe Island Woodhen Tricholimnas sylvestris (Sclater). Biological Conservation 34:55–95.

Miller, P. S. 1994. Is inbreeding depression more severe in a stressful environment? Zoo Biology 13:195–208.

Miller, P. S., and P. W. Hedrick. 1993. Inbreeding and fitness in captive populations: lessons from Drosophila. Zoo Biology 12:333–351.

Mills, L. S., and P. E. Smouse. 1994. Demographic consequences of inbreeding in remnant populations. American Naturalist 144:412–431.

Mirande, C., R. Lacy, and U. Seal. 1991. Whooping crane (Grus americana) conservation viability assessment workshop report. Captive Breeding Specialist Group, World Conservation Union–Species Survival Commission, Apple Valley, Minnesota.

Myers, N. 1987. The extinction spasm impending: synergisms at work. Conservation Biology 1:14–21.

Newmark, W. D. 1995. Extinction of mammal populations in western North American national parks. Conservation Biology 9:512–526.

Nunney, L., and K. A. Campbell. 1993. Assessing minimum viable population size: demography meets population genetics. Trends in Ecology and Evolution 8:234–239.

O'Brien, S. J., D. E. Wildt, D. Goldman, C. R. Merril, and M. Bush. 1983. The cheetah is depauperate in genetic variation. Science 221:459–462.

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.

Packer, C., A. E. Pusey, H. Rowley, D. A. Gilbet, J. Martenson, and S. J. O'Brien. 1991. A case study of a population bottleneck: lions of the Ngorongoro Crater. Conservation Biology 5:219–230.

Pettersson, B. 1985. Extinction of an isolated population of the Middle Spotted Woodpecker Dendrocopos medius (L.) in Sweden and its relation to general theories of extinction. Biological Conservation 32:335–353.

Pounds, J. L., and M. L. Crump. 1994. Amphibian declines and climate disturbance: the case of the golden toad and the harlequin frog. Conservation Biology 8:72–85.

Ralls, K., and J. D. Ballou. 1983. Extinction: lessons from zoos. Pages 164–184 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, editors. Genetics and conservation: a reference for managing wild animal and plant populations. Benjamin/Cummings, Menlo Park, California.

Ralls, K., K. Brugger, and A. Glick. 1980. Deleterious effects of inbreeding in a herd of captive Dorcas gazelle. International Zoo Yearbook 20:137–146.

Ralls, K., J. D. Ballou, and A. R. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. Conservation Biology 2:185–193.

Rich, W. H. 1939. Local populations and migration in relation to the conservation of Pacific salmon in the western states and Alaska. Contribution no. 1 Fish Commission of Oregon.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board Canada. 9:559–623.

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Pages 27–160 in R. C. Simon and P. A. Larkin, editors. The stock concept in Pacific salmon. University of British Columbia Press, Vancouver, British Columbia.

Riddell, B. E. 1993. Spatial organization of Pacific salmon: what to conserve? Pages 23–41 in J. Cloud, and G. H. Thorgaard, editors. Genetic conservation of salmonid fishes. Plenum Press, New York.

Roelke, M. E., J. S. Martenson, and S. J. O'Brien. 1993. The consequences of demographic reduction and genetic depletion in the endangered Florida panther. Current Biology 3:340–350.

Rosenzweig, M. L., and C. W. Clark. 1994. Island extinction rates from regular censuses. Conservation Biology 8:491–494.

Ryman, N., and L. Laikre. 1991. Effects of supportive breeding on the genetically effective population size. Conservation Biology 5:325–329.

Ryman, N., P. Jorde, and L. Laikre. 1995. Supportive breeding and variance effective population size. Conservation Biology 9:1619–1628.

Schemske, D. W., B. C. Husband, M. H. Ruckelshaus, C. Goodwillie, I. M. Parker, J. G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584–606.

Seal, U. S. 1992. Genetic management strategies and population viability of the Florida panther (Felis concolor coryi). Report to the U.S. Fish and Wildlife Service, Captive Breeding Specialist Group, World Conservation Union–Species Survival Commission, Apple Valley, Minnesota.

Seal, U. S. 1994. A plan for genetic restoration and management of the Florida panther (Felis concolor coryi). U. S. Fish and Wildlife Service, Captive Breeding Specialist Group, World Conservation Union–Species Survival Commission, Apple Valley, Minnesota.

Seal, U. S., E. T. Thorne, M. A. Bogan, and S. H. Anderson, editors. 1989. Conservation biology and the black-footed ferret. Yale University Press, New Haven, Connecticut.

Shaffer, M. 1981. Minimum population sizes for species conservation. BioScience 31:131-141.

Shaffer, M. 1987. Minimum viable populations: coping with uncertainty. Pages 69-86 in M. Soulé, editor. Viable populations for conservation. Cambridge University Press, New York.

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

Smith, T. B., and R. K. Wayne. 1996. Molecular genetic approaches in conservation. Oxford University Press, New York.

Soulé, M. E., and G. P. Zegers. 1996. Phenetics of natural populations. V. Genetic correlates of phenotypic variation in the pocket gopher *Thomomys Bottae* in California. Journal of Heredity, in press.

Soulé, M. E., D. T. Bolger, A. C. Alberts, R. Sauvajot, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2:75-92.

Taylor, B. L. 1995. The reliability of using population viability analysis for risk classification of species. Conservation Biology 9:551-558.

Tuljapurkar, S., and S. H. Orzak. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. Theoretical Population Biology 18:314-342.

Vrijenhoek, R. C. 1994. Genetic diversity and fitness in small populations. Pages 37-53 in V. Loeschcke, J. Tomiuk, and S. K. Jain, editors. Conservation genetics. Birkhäuser Verlag, Basel.

Wayne, R. K., D. A. Gilbert, N. Lehman, K. Hansen, A. Eisenhawer, D. Girman, L. D. Mech, P. J. P. Gogan, U. S. Seal, and R. J. Krumenaker. 1991. Conservation genetics of the endangered Isle Royale gray wolf. Conservation Biology 5:41-51.

Widén, B. 1993. Demographic and genetic effects on reproduction as related to population size in a rare, perennial herb, *Senecio integrifolius* (Asteraceae). Biological Journal of the Linnean Society 50:179-195.

Wielebowski, N. 1996. Reassessing the relationship between juvenile mortality and genetic monmorphism in captive cheetahs. Zoo Biology 15:353-369.

Withler, F. 1982. Transplanting Pacific salmon. Canadian Tech. Rep. Fish. Aquat. Sci. 1079.

Wolfe, L. M. 1993. Inbreeding depression in *Hydrophyllum appendiculatum*: role of maternal effects, crowding, and parental mating history. Evolution 47:374-386