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Ecology and Management of Small Populations

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INTRODUCTION

HUMAN-CAUSED CHANGES to natural landscapes are **fragmenting wildlife habitats** and causing many species to decline, often **creating small, isolated populations.** Management concerns for small populations are frequently unlike those for large or thriving populations. When the small population of concern is a **threatened or endangered species,** management is a high-profile process, occurring in a regulatory environment and typically involving intensive management practices (Temple 1978*b*, Clark et al. 1994, Scott et al. 1994). In many cases, issues faced by managers of small populations are intensified versions of tasks important for managing any wildlife population: regulating rates of birth, dispersal, and mortality; maintaining habitat quantity and quality; and managing disease, predators, competitors, and other **extrinsic factors.** These issues often become critically important in management of small populations, with limited time and few second chances for management to succeed. In addition, managers must cope with a number of questions more specific to small populations, such as avoiding genetic problems, doing viability analyses, and stimulating population growth.

In this chapter, we address a number of issues of special interest in **management of small populations.** First, we summarize **biological and legal criteria** for identifying small populations, and review the range of population sizes that are considered "**small.**" We then discuss factors that affect whether small populations will persist or become extinct. Finally, we provide management guidelines for small populations, including a detailed description of viability assessment in general, and population viability analysis in particular, as practical, powerful tools for planning the management of small populations.

WHAT IS A SMALL POPULATION?

There are few precise definitions of a "**small population.**" The reluctance to assign specific criteria is no doubt because so many variables are involved when considering population size across a wide range of species and conditions.

The Oxford English Dictionary (Simpson and Weiner 1989, XV:767) **defines "small" as:** "of limited size; of comparatively restricted dimensions; not large in comparison with other things, esp. of the same kind." This definition highlights the comparative nature of any criteria; except in extreme cases (what Scott et al. [2001] called **vanishingly small populations**), small size is a relative concept. Whether or not a population is considered small is dependent on a series of comparisons with populations of conspecifics, similar species, historical population sizes, and even arbitrary management standards. For an **exploited species** such as the canvasback (*Aythya valisineria*), conservation plans may call for corrective management to be implemented when population sizes decrease to the tens of thousands. In contrast, conservation efforts for **threatened species** may be delayed until the population falls below 100 or is putatively extinct (e.g., ʻōʻū [*Psittirostra psittacea*]). Thus, an attempt to define a universal criterion for small based on numbers may be useful as a heuristic exercise, but should not be interpreted too strictly (Box 35.1).

The definition of a small population also may be influenced by a species' life-history characteristics. In general, **extinction probability** increases as population size decreases, an idea deeply rooted in wildlife biology and ecology (e.g., Leopold 1933, MacArthur and Wilson 1967). In some (but not all) cases, **restricted geographic range or local endemism** can serve as proxies for small population size (Channell and Lomolino 2000, Purvis et al. 2000). Populations with higher variance in population growth rate relative to mean population growth rate will have to be larger to avoid extinctions (Lande 1993; Fagan et al. 1999, 2001). **Species attributes** such as litter or clutch size, age at first reproduction, and intervals between births may be useful for predicting population growth rate or variation in growth rate and, therefore, vulnerability of a population (Purvis et al. 2000, Fagan et al. 2001).

By contrast, the use of secondary surrogates such as home range size, group size, or body size as general indicators of **extinction vulnerability** has been largely unsuccessful because correlations are weak and inconsistent (e.g., large-bodied animals tend to show lower variation in numbers, but also lower population growth rates; Lawton 1995). Some animals may be more vulnerable because of their sensitivity to **anthropogenic threats,** limited dispersal capability, narrow habitat requirements, and the extent to which a species is harvested or persecuted by humans, rather than because of body size or home range size per se. Vulnerability also may derive, in part, from particular **behavioral attributes** (Reed 1999); for example, species might be more vulnerable

BOX 35.1. THE "50–500 RULE"

As a historical footnote while considering the meaning of a small population, it is worth reviewing the famous "50–500 rule." This rule of thumb emerged from a meeting on the application of conservation genetics to wild species (Franklin 1980, Soulé 1980, Frankel and Soulé 1981), and over the next decade was accepted into the Puerto Rican parrot (*Amazona vittata*) recovery plan (U.S. Fish and Wildlife Service 1987) and a number of other management plans and biological opinions (e.g., U.S. Fish and Wildlife Service 1998). In essence, the rule provides a minimum genetic effective size for short-term and long-term protection, respectively.

An effective size of 50 was proposed as a minimum to protect against short-term loss of fitness due to inbreeding, based on empirical observations of the decrease in fitness-related traits with incremental inbreeding in a variety of animal species. Several caveats implicit in the original rule were lost as management was applied (Soulé 1987, Soulé and Mills 1992). For example, 50 is the *genetic effective size (Ne)*, which is only about 20–33% that of the total population size (Frankham et al. 2002); thus, a Ne of 50 would translate to 150–250 or so actual animals. Second, the rule was proposed as a short-term guideline for captive breeding and similar "holding operations," not for long-term survival of wild populations, which would have many other factors affecting their persistence. Third, this was a rule based on genetic factors, not incorporating other factors that would increase the minimum necessary size for persistence. Based on these considerations, it is untenable to argue that an actual population size of 50 is sufficient as a rule to support any wildlife population into the foreseeable future.

The 500 number was proposed as the minimum size necessary to ensure long-term maintenance of genetic variation, thereby preserving evolutionary options for future adaptation. In more formal terms, the number was the estimated minimum genetic effective size where the loss of additive genetic variation of a quantitative character due to genetic drift would be balanced by new variation due to mutations. This number has received serious scrutiny by population geneticists, with arguments being made for minimum population sizes ranging up to 5,000 or more (Frankham et al. 2002). This debate will likely continue (Allendorf and Ryman 2002), but there is little doubt that the *actual* (as opposed to genetic effective) population size necessary to maintain evolutionary potential for the long term should be thousands of individuals and not hundreds.

if they show Allee effects (reduced survival or reproduction at small numbers), naiveté toward predators (e.g., dodo [*Raphus cucullatus*]), or aggregated dispersion (e.g., passenger pigeon [*Ectopistes migratorius*]). The final utility of these ecological and life-history characteristics as **predictors of extinction** depends on the specific context of the environment and the species in question (Tracy and George 1992, Belovsky et al. 1999, Channell and Lomolino 2000). For example, vulnerabilities of primates and carnivores were underestimated by a model based on species characteristics in cases where the species had lost habitat, been commercially overexploited, or where problems had been created by **exotic species** (Purvis et al. 2000).

One way of summarizing these complex factors is to survey many species and ask how large populations must be in order to be considered likely to persist. Two recent **meta-analyses** of thousands of studies for hundreds of species conclude that the median population size for expected high likelihood of persistence (>80%) for ≥20–100 years was about 1,400–4,000 individuals (Brook et al. 2006, Traill et al. 2007). Although these would not be robust "**magic numbers**" for precise conservation targets, they provide rough rules-of-thumb for when a population might be considered too "small" for persistence.

Finally, any consideration of "small" should not be limited to **persistence criteria,** but also should include **ecological function** of the species, and long-term ability to **adapt and evolve.** Both of these numbers will likely be much larger than the size necessary to support a population in the short term. We know of no generalizations for the population size of a species required for it to carry out its ecological role, but note by example that population size for a strongly interacting species to carry out its ecological function (e.g., prairie dogs [*Cynomys* sp.] or elk [*Cervus canadensis*] as habitat modifiers, wolves [*Canis lupus*] as top-down predators, or small mammals as prey) will certainly be much larger than the size needed for persistence per se. For evolutionary potential, one proposal would scale a threshold according to the population size necessary to retain 95% of the heterozygosity of the population for 100 years (Allendorf and Ryman 2002). What this size will be depends on mating system and other characteristics affecting the generation time and **genetic effective population size** (see Chapter 22, Volume 1); Traill et al. (2010) suggest that number to be roughly 5,000 adult individuals or more.

Guidelines for "Small" from Categorization Systems

Guidelines to what is considered "small" have been established by agencies. For example, the **International Union for the Conservation of Nature** (IUCN, or World Conservation Union) has developed a categorical system for assigning risk based in part on small population size ("Rule-of-Thumb" approach discussed later in chapter). Species with small, stable populations are considered "**critically endangered**" if their populations fall below 50 mature individuals, "**endangered**" if their populations have <250 mature individuals, and "**vulnerable**" if they consist of ≤1,000 mature individuals. Small, declining populations have higher threshold values for each category (Table 35.1; also see "Rules-of-Thumb" in section on "Other Approaches to Assess Viability").

In the United States, a comprehensive system of assessing the conservation status and extinction risk for species has been developed by the **Natural Heritage Network and The Nature Conservancy** (Master et al. 2000). The heritage ranking system is based on the perceived vulnerability of a species to extinction, taking into consideration both **intrinsic risks and external threats.** A species is considered "**critically imperiled**" if fewer than 1,000 individuals exist across its range; at the other end of the spectrum are "**apparently secure**" species with ≥10,000 individuals (Table 35.2). Although these categories are not based on scientific criteria, they provide insights into what may be considered a "**small population**" for management purposes.

Finally, a measure of a "small population" might be extracted from listings under the **Endangered Species Act** (ESA). Between 1985 and 1991, the median population size

Table 35.1. International Union for Conservation of Nature (IUCN) Red List criteria that are relevant to defining small populations

Red list category	Very small population	Small population and declining
Critically endangered	<50 mature individuals	<250 mature individuals, population declining
Endangered	<250 mature individuals	<2,500 mature individuals, population declining
Vulnerable	<1,000 mature individuals	<10,000 mature individuals, population declining

From IUCN (2001).

Table 35.2. Natural Heritage Program conservation status rank definitions

Rank	Definition
1	Critically imperiled. Typically ≤5 occurrences or ≤1,000 individuals.
2	Imperiled. Typically 6–20 occurrences or 1,000–3,000 individuals.
3	Vulnerable. Rare; typically 21–100 occurrences or 3,000–10,000 individuals.
4	Apparently secure. Uncommon, but not rare; some cause for long-term concern; usually >100 occurrences and >10,000 individuals.
5	Secure. Common; widespread and abundant.

From Master et al. (2000).

for threatened and endangered species at time of listing was 1,075 individuals for vertebrates, 999 for invertebrates, and 120 for plants (Wilcove et al. 1993).

Naturally Small versus Declining Populations

Not all small populations have declined. In fact, a longstanding generalization in community ecology (tracing back at least to Preston [1948]) holds that many, perhaps most, species in a community are relatively rare. Indeed, **naturally small populations** often persist on true islands, or island-like continental environments (Walter [1990] provided an example with the Socorro Island hawk [*Buteo jamaicensis socorroensis*]). Other wildlife species that typically occur in naturally small populations include top carnivores such as wolverines (*Gulo gulo*), large animals such as mountain sheep (*Ovis canadensis*), and species restricted to small areas of habitat (e.g., big-eared kangaroo rat [*Dipodomys venustus elephantinus*]). These populations may share some risk factors with declining populations, but more likely have distinctive life-history features that allow them to persist (Angermeier 1995, Fagan et al. 2001). **Management** of naturally small populations may focus primarily on maintaining the status quo: supporting natural disturbance regimes, avoiding habitat loss or degradation, and preventing the introduction of competitors, predators, parasites, or diseases. Also, naturally "small" populations are only locally small, but are connected to a greater **metapopulation;** in these cases, connectivity also should be retained.

In contrast to naturally small populations are species that were once common or widely distributed, but are now restricted to small, isolated populations following a reduction in population size. A **population's decline** may be due to deterministic drivers such as habitat fragmentation or loss, introduced species, disease, overharvest, or a combination of factors, but the result is a population that is usually at **increased risk of extinction** due to both **deterministic and stochastic factors** (Clark et al. 1990, Reed et al. 2002, Mills 2007). Native birds of the Hawaiian Islands and Guam (Scott et al. 1986, Savidge 1987) are examples of situations where entire avifaunas have been placed at risk because of a combination of factors. Additional management activities may be required, because small populations are more vulnerable to extinction (see below).

LEGAL MANDATES FOR MANAGEMENT OF SMALL POPULATIONS

In the United States, there are **53 federal statutes** providing for conservation of species through restrictions on take and commerce, conservation of wildlife habitat, conservation of endangered species, conservation of both species and habitat, and control of "problem wildlife" (Box 35.2). Detailed descriptions of these statutes and treaties can be found in Goble and Freyfogle (2002*a*, *b*). These statutes, while providing the legal framework for protecting species, deal with issues of population size only vaguely; none incorporate the phrase "small population size" or define when population size reaches the point at which management is mandated. In contrast, the **Marine Mammal Act** (Section 2:130) explicitly addresses the population size necessary to maintain ecosystem integrity, and states that "population stocks should not be permitted to diminish beyond the point at which they cease to be significant functioning elements of the ecosystem of which they are a part and, consistent with this major objective, they should not be permitted to diminish below their **optimum sustainable populations.**" Further, to reduce the chance that stocks will be overharvested, the concept of uncertainty has been incorporated into the day-to-day implementation of the Marine Mammal Act (Taylor et al. 2000). Next, we describe in more detail the 3 statutes of greatest relevance for conservation of small wildlife populations in North America.

Endangered Species Act

Foremost in the United States among federal wildlife statutes that specifically address the management needs of "small populations" is the **Endangered Species Act** of 1973 with its subsequent amendments (Goble and Freyfogle 2002*b*). The Act provides for the protection and recovery of **species** (defined as species, subspecies, and distinct population segments for vertebrates, and as species and subspecies for plants and invertebrates). The Act's objective was to conserve "to the extent practicable the various species of fish and wildlife and plants facing extinction throughout all or a significant part of their range" (U.S. Fish and Wildlife Service [USFWS] 1973:1). **No numerical criteria** for either population size or trends are specified in the ESA as a threshold for listing a species as endangered or threatened. The number of individuals at the time of listing varies by orders of magnitude even within a class of organisms (Wilcove et al. 1993). For example, the Inyo California towhee (*Pipilo crissalis eremophilus*) was listed as threatened when it reached a population size of 175 individuals, whereas the coastal California gnatcatcher (*Polioptila californica californica*) still numbered in the thousands when it was listed as endangered. Similarly, there are **no demographic criteria** for down-listing or delisting species beyond a directive for "objective, measurable criteria which, when met, would result in a determination . . . that the species should be removed from the list" of threatened and endangered species (Goble and Freyfogle 2002*a*:354).

Species at Risk Act

The recently passed **Species at Risk Act** (SARA) **of Canada** (S.C. 2002, c.29) provides for the protection of rare wildlife, which includes species, subspecies, variety, or geographically or genetically distinct populations. The **criteria for listing or delisting** a species in Canada are more similar to IUCN criteria and more specific than the ESA. In 1988, the Council

BOX 35.2. FEDERAL STATUTES RELATED TO THE MANAGEMENT OF WILDLIFE

1. Conserving Species through Restrictions on Take and Commerce
    - a. Lacey Act, 1900, 1981
    - b. Migratory Bird Treaty Act, 1918
    - c. Tariff Act of 1930
    - d. Bald and Golden Eagle Protection Act, 1940, 1962
    - e. Act Prohibiting the Use of Aircraft and Motor Vehicles to Hunt Feral Horses and Burros, 1959
    - f. Horses and Burros, 1959
    - g. Airborne Hunting Act, 1971
    - h. Wild Free-Roaming Horses and Burros Act, 1971
    - i. Marine Mammal Protection Act, 1972
    - j. Magnuson–Stevens Fisheries Conservation and Management Act, 1976
    - k. Neotropical Migratory Bird Conservation Act, 1999
    - l. Wild Exotic Bird Conservation Act, 1992
    - m. African Elephant Conservation Act, 1988
    - n. Asian Elephant Conservation Act, 1998
    - o. Rhinoceros and Tiger Conservation Act, 1998
    - p. Great Ape Conservation Act, 2000
2. Conserving Wildlife Habitat
    - a. Federal Wildlife Refuges
    - b. Migratory Bird Conservation Act, 1929
    - c. Migratory Bird Stamp Act, 1934
    - d. Wetlands Loan Act, 1961
    - e. Refuge Revenue Sharing Act, 1935, 1964
    - f. Refuge Trespass Act, 1948
    - g. Refuge Recreation Act, 1962
    - h. Refuge Administration Act, 1966
    - i. National Marine Sanctuaries Act, 1992
    - j. National Wildlife Refuge System Improvement Act, 1997
3. Funding State Acquisition of Habitat
    - a. Federal Aid in Wildlife Restoration Act, 1937 (The Pittman–Robertson Act)
    - b. Federal Aid in Fish Restoration Act, 1950 (Dingell–Johnson Act)
    - c. Land and Water Conservation Fund Act, 1964
    - d. Fish & Wildlife Conservation Act, 1980
4. Consideration of the Effect of Federal Actions on Wildlife Habitat
    - a. Fish and Wildlife Coordination Act, 1934, 1946, 1958
    - b. National Environmental Policy Act, 1969
5. Planning and Coordination
    - a. The Anadromous Fish Act, 1965
    - b. Sikes Act Extension, 1974
6. Conserving Endangered Species
    - a. Endangered Species Act, 1973
7. Conservation of Both Species and Habitat—Federal Lands
    - a. National Park Service
        - i. Antiquities Act, 1906
        - ii. National Park Service Organic Act, 1916 and General Authorities Act, 1970
    - b. U.S. Forest Service
        - i. National Forest Service Organic Act, 1897
        - ii. Multiple-Use Sustained-Yield Act, 1960
        - iii. National Forest Management Act, 1976
    - c. Bureau of Land Management
        - i. Federal Land Policy and Management Act, 1976
        - ii. Public Rangelands Improvement Act, 1978
    - d. Military Lands
        - i. Sikes Act, 1960, 1997
    - e. Preservation Land Systems
        - i. Wilderness Act, 1964
        - ii. Wild and Scenic Rivers Act, 1968
    - f. Federal Waters
        - i. Rivers and Harbors Act, 1899
        - ii. Federal Power Act, 1920
        - iii. Federal Water Pollution Control Act, 1972
8. Conservation of Both Species and Habitat—Private Lands
    - a. Wetlands
        - i. Federal Water Pollution Control Act, 1972
        - ii. "Swampbuster" Provisions, 1985, 1990, 1996
        - iii. Coastal Barrier Resources Act, 1982
    - b. Uplands
        - i. Conservation Reserve Program, 1985
        - ii. Environmental Easement Program, 1990
        - iii. Forest Legacy Program, 1990
9. Problem Wildlife
    - a. Lacey Act, 1900
    - b. Animal Damage Control, 1931
    - c. Nonindigenous Aquatic Nuisance Prevention and Control Act, 1990

From Goble and Freyfogle (2002a).

of Canadian Wildlife Ministers signed an agreement establishing the **Recovery of Nationally Endangered Wildlife** (RENEW) program (Scudder 1999). The objectives of RENEW are to prevent the extinction of species, prevent additional species from becoming threatened or endangered, reintroduce extirpated species, establish recovery plans to remove species from the threatened and endangered list, and prepare recovery plans for all threatened and endangered species (Canadian Wildlife Service 2001).

CITES

The Endangered Species Act of 1973 also included provisions for increased **protection of endangered and threatened species worldwide** (Bean 1983). As of 2 October 2009, 30% of listed species were outside the United States (USFWS 2009). The ESA implemented the **Convention on International Trade in Endangered Species of Wild Flora and Fauna** (CITES) in the United States and provided a program to encourage foreign governments to establish programs for conservation of species (Bean 1983). Species listed under CITES cannot be transported between countries without special permit. The **criteria for listing** are only vaguely defined and the decision to list a species depends largely on consensus of the parties. Mexico also is signatory to CITES.

The **United States/Mexico Joint Committee on Wildlife Conservation** was established in 1974 to help address the question of vulnerable species. This agreement provides the basis for cooperation on conservation efforts for species occurring in both nations, such as sharing survey information and cooperation on recovery efforts for species. However, it is vague about defining a small population.

FACTORS AFFECTING PERSISTENCE IN SMALL POPULATIONS

Deterministic Factors

In managing a small and declining population, the most important factors to consider are what caused the population to become small, and how to reverse the decline. Whether the cause of decline was habitat loss, overharvest, exotic species, change in disturbance regime, or some combination of these or other causes, the perturbations that led to the population becoming small are of paramount importance (Caughley and Gunn 1996) and greatly influence the possibility of recovery (Abbitt et al. 2000, Miller et al. 2002). These factors are "**deterministic,**" indicating the outcome for the population can be expected to follow in a relatively predictable way. Thus, deterministic factors that affect population growth in known ways are distinguished from "**stochastic**" or random factors that also affect small populations.

Stochastic Factors

Unfortunately, when a population becomes small it becomes particularly susceptible to a host of other threats that interact with and exacerbate problems caused by deterministic factors. Thus, for small populations, even if the deterministic problems were reversed so the population achieved a positive average population growth, the population could still be driven toward extinction. Factors are called "stochastic" because they have a large element of randomness in how they affect any particular population.

Two important points emerge from an understanding of stochastic factors: (1) with all else equal, small populations are more likely to become extinct than large ones; and (2) with all else equal, populations with large variation in vital rates are more likely to become extinct than those with small variation. There are 3 main types of stochasticity affecting **population persistence** (Shaffer 1987): demographic, environmental, and genetic. The operation and effect of stochastic factors on populations are less intuitive than deterministic factors; therefore, we explain how they affect small populations (see Mills 2007 for more details).

Demographic Stochasticity

Demographic stochasticity arises from inevitable deviations around mean birth and death rates because these rates are probabilistic. For small populations, demographic stochasticity causes variation in population growth even in a constant environment, with no change in mean birth or death rates. One of the easiest ways to understand demographic stochasticity and its special effects on small populations is by example. If you toss a fair coin, the expected probability of heads is a constant 50%. But if you toss the coin only 3 times, you cannot possibly get 50% heads: you can only get 0%, 33%, 67%, or 100% heads, by chance! Even if you tossed it 4 times, you would not be too surprised to get something other than 50:50. However, if you tossed the coin 100 times you would expect the percentage of heads to be much closer to 50%, and if you tossed it 1,000 times you would be highly confident of converging on 50%, the expected probability of heads.

Consider how this analogy would apply to **sex ratios,** which are typically expected to be close to 50:50 at birth if there are many births occurring in the population. If, however, there are few births because of small population size, stochasticity could easily result in a marked deviation from the expected 50:50 ratio; this stochastic change could impair the population's ability to recover. Similarly, survival and birth rates in a small population could deviate widely from the expected mean by chance alone. Thus, demographic stochasticity **can affect sex ratio, reproduction, and/or survival,** causing each to be more or less than the mean expectation. Therefore, even if the environment is relatively constant and birth and death rates are such that average population growth should be positive, demographic stochasticity in a small population could still cause a decline toward extinction. An often-cited example of the effects of demographic stochasticity in sex ratio is the extinction of the dusky seaside sparrow (*Ammospiza maritime nigrescens*) when all of the last 6 survivors happened to be males (James 1980, Avise and Nelson 1989, Post and Greenlaw 1994).

Just as a coin toss converges on 50:50 with many tosses, demographic stochasticity is minimized when abundance exceeds about 100 individuals (Morris and Doak 2002), so only relatively small populations are highly likely to decline from this factor alone. In some cases, **individual variation** is characterized as stochastic to ease analytical tractability when really there are **deterministic drivers,** perhaps due to maternal provisioning, genetic makeup, territory quality, or other factors. The extent to which this occurs can affect the influence of demographic stochasticity (McCarthy et al. 1994, Fox and Kendall 2002, Kendall and Fox 2002).

Environmental Stochasticity

In contrast to demographic stochasticity, **environmental stochasticity** produces random changes in mean vital rates for all individuals. Environmental stochasticity results from factors that are **extrinsic to the population.** Although environmental factors can be either physical or biotic, they occur in unpredictable patterns. The most obvious form of environmental stochasticity is climate, including normal vagaries of temperature and other weather-related phenomena, such as severe storms. Regardless of the underlying (and usually unknown) mechanism, mean vital rates for all animals in the population and, therefore, population growth rate, vary over time and space in unpredictable ways. Unlike demographic stochasticity, environmental stochasticity does not disappear in large populations. For example, a change in population growth rate from a 2% increase to a 2% decrease/year translates into changes in population size whether there are 50 or 500 animals in the population.

An underappreciated result of environmental stochasticity is that it can make the most likely (stochastic) growth rate for a population be greater or less than the average growth rate without stochasticity (Doak et al. 2005, Morris et al. 2008). Consider a simple case of a population whose **annual population growth rate** is equally likely to be $\lambda = 1.6$ or $\lambda = 0.6$ in any given year (**$\lambda = 1.0$ is stable**). The arithmetic mean of the growth rate is 1.1 [$= (1.6 + 0.6)/2$], indicating an increasing population, but the stochastic growth rate is 0.98 ($\lambda = \sqrt{1.6 \times 0.6}$), meaning the most likely trajectory for this fluctuating population is to decline. This phenomenon could lead a manager to believe a population is likely to increase, based on the mean population growth derived from count data or matrix models, when actually it is most likely to decrease in a variable environment (Fig. 35.1). Although this simple example of population growth without age structure shows stochasticity decreasing population growth, negative correlations among vital rates could actually cause variation to increase population growth (Doak et al. 2005).

A practical point to remember about environmental stochasticity as estimated from field data is that it has an **associated sampling error.** In essence, sampling variation adds noise to the estimate of environmental variation. Thus, total variance should be partitioned into true process variance (**spatial and temporal variation**) distinct from the "**noise**" of sampling variance. The use of total variance for environmental stochasticity, instead of true process variance, will make nature seem more "variable" than it actually is. The artificially inflated variance will both reduce confidence in the actual trend, and will lead to biased-high predictions of extinction in population viability analysis (Ludwig 1999).

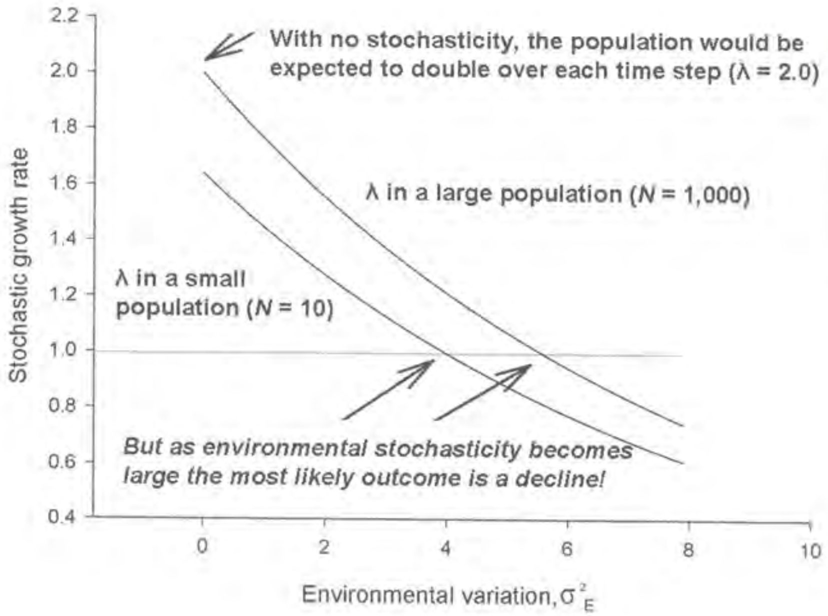

Fig. 35.1. An example of environmental stochasticity (with no covariation among vital rates or over time) decreasing the expected population growth rate relative to the mean rate. The upper curve shows the reduction in a large population ($N = 1{,}000$). The lower curve shows the further decrease in a small population ($N = 10$) due to demographic stochasticity. *Modified from Mills (2007).*

Methods for partitioning total variance into the component process versus sampling variation are discussed in Thompson et al. (1998) and White (2000*b*).

Finally, we note that populations can be exposed to stochastic events that are extreme beyond the tails of expected environmental stochasticity. These events are called "**catastrophes**" or "**bonanzas,**" and can have profound effect on persistence of small populations (Shaffer 1987, Morris and Doak 2002). For example, a 1963 hurricane decimated the last Laysan teal (*Anas laysanensis*) population; volcanic eruptions in Japan almost destroyed the last colony of the short-tailed albatross (*Phoebastria albatrus*); and a severe winter coupled with overbrowsing killed all but 50 of the 6,000 reindeer (*Rangifer tarandus*) on St. Matthew Island (Simberloff 1988).

Genetic Stochasticity

The third stochastic factor refers to **random loss of alleles** (alternative forms of a gene), and the subsequent effects on population dynamics in small populations. **Genetic stochasticity** arises from **genetic drift,** the process whereby random inheritance of alleles in a small, randomly mating population leads to the "drifting" of the frequency of alternative alleles toward either 1.0 or 0.0, and an accompanying increase in homozygosity. Vertebrates carry enough **deleterious alleles** ("lethal equivalents per individual") to kill each individual about 3 times over (reviewed by Keller 1998), but in large populations natural selection holds them at low frequency, and their recessive nature means their effects are masked by a nonharmful allele. However, genetic drift can lead to reduced survival or reproduction via inbreeding depression when these deleterious alleles become expressed as **homozygotes.**

Loss of **heterozygosity** and expression of inbreeding depression due to genetic drift in small wildlife populations are well-established processes that can affect both captive and wild populations (Mills and Tallmon 1999). Like any other process (predation, disease, weather events, etc.), the effects of **inbreeding depression** on population dynamics will range from nonexistent to strong, for any particular population. Reviews indicate that a majority of small wildlife populations may exhibit inbreeding depression, and reductions in fitness can be substantial (Crnokrak and Roff 1999, Keller and Waller 2002).

If genetic drift and inbreeding depression decreases viability of a small population, the good news is that these effects can, in principle, be reversed by **genetic rescue** (Tallmon et al. 2004) through immigration of individuals from outside the population. Genetic rescue leads to a "breaking" of inbreeding depression and an increase in population growth by more than the demographic contribution of the immigrants; therefore, it can be an effective management action (Chapter 36, This Volume). In an excellent example, a population of bighorn sheep (*O. canadensis*) founded by 12 individuals and isolated for 10–12 generations, showed inbreeding depression followed by 23–257% increase in fitness-related traits following experimental restoration of immigration (Hogg et al. 2006). If genetic rescue is accompanied by considerations to also restore historical levels of diversity to maintain evolutionary potential efforts and prevent genetic swamping, then the small population will be the recipient of **genetic restoration** (Hedrick 2005).

Genetic restoration raises the important point that loss of genetic variation in small populations also depletes the raw material of evolution underlying a population's capacity to adapt to changes in climate, habitat, competitors, disease, etc. If it is lost in small populations, the ability to survive future changes can be compromised even if the population subsequently recovers to its former size (Soulé 1980, Frankham et al. 2002). As an example, Botta's pocket gopher (*Thomomys bottae*) populations that have low genetic variation are actually able to accept reciprocal skin grafts from individuals within their population; populations with high variation reject the grafts (Sanjayan et al. 1996). This extreme consequence of loss of variation, resulting in an individual not being able to distinguish self from nonself, implies that ability to recognize and destroy intruder viruses, microbes, and other diseases will be compromised.

PREDICTING THE RISKS OF SMALL POPULATION SIZE

The Extinction Vortex

We have stressed that both deterministic and stochastic factors affect the likelihood of a small population declining, or becoming extinct. The interaction of all of these factors is portrayed by the **extinction vortex** (Fig. 35.2). This captures the idea that primary drivers of concern for declining and/or small populations are deterministic **human-caused perturbations.** How the perturbation affects a particular population depends on its **structure** (life-history characteristics, age structure, behavioral interactions, distribution, physiological status, etc.), and on the **environment** (habitat, weather, competition, predators, food abundance, etc.). These perturbations can decrease **vital rates** (reproduction and survival), thereby decreasing both population growth rate and population size. Each turn of the feedback cycle increases extinction probability because decreased population size and growth rate lead to increased effects of inbreeding depression and stochastic events, further decreasing population size and growth. The extinction vortex emphasizes the need to consider the relative importance of these different factors and how they interact in a particular case (Gilpin and Soulé 1986, Lande 1988, Soulé and Mills 1992, Mills and Smouse 1994).

Greater prairie-chickens (*Tympanuchus cupido*) in Illinois provide an example of the **extinction vortex in action** (Bouzat et al. 1998*a*, *b*; Soulé and Mills 1998; Westemeier et al. 1998; Bouzat et al. 2009). As native grasslands have been in-

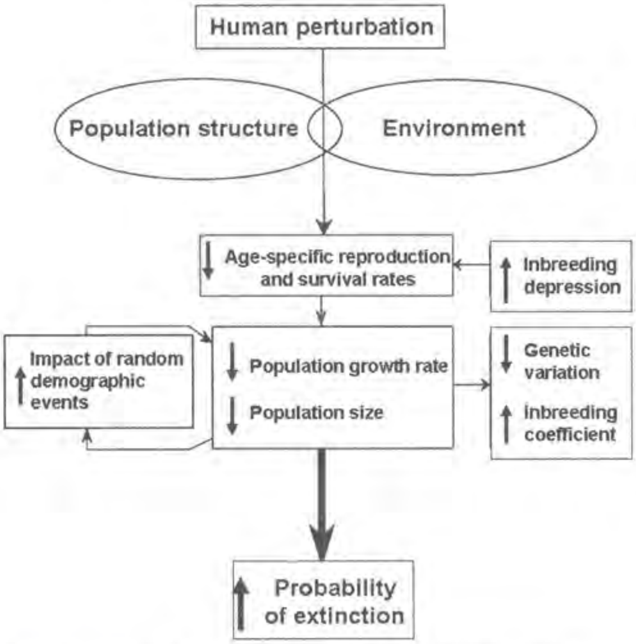

Fig. 35.2. A simplified representation of the extinction vortex. *Adapted from Soulé and Mills (1998).*

creasingly fragmented, the Illinois population of the greater prairie-chicken **became small and isolated** from other populations, declining from about 2,000 individuals in the early 1960s to 50 birds by the early 1990s. Although habitat loss and alteration, and associated increases in predators, clearly caused the decline, stochastic factors became relevant at small population size. In particular, **genetic variation** for Illinois prairie-chickens **declined** relative to both historical samples collected from that population and to populations in neighboring states, which had remained relatively large and widespread. **Translocations** of prairie-chickens from neighboring states from 1992 to 1996 appeared to lead to successful **genetic restoration,** as genetic diversity was restored to historic levels, **inbreeding coefficients decreased** (at least to some extent), and significant **increases in both fertility and hatchability** rates indicated that inbreeding depression was ameliorated. Nevertheless, in a somber note that underscores the difficulty in breaking out of the extinction vortex, the transient increases in population size following translocation have stalled, probably due to limitations in habitat availability and habitat quality. In short, this example demonstrates that **management actions** can be taken to redirect population growth away from the extinction vortex, but these will ultimately be successful only with continued vigilance in providing adequate habitat and addressing deterministic causes of declines (Maehr and Lacy 2002, Bouzat et al. 2009).

The Process of Viability Assessment

Wildlife viability assessment (Box 35.3) formalizes evaluation of the processes of the extinction vortex. It places intuition, field data, and theory into an operational framework to allow assessment of the factors that caused decline and that may cause further decline in the future. It is a framework for incorporating multiple, interacting processes; therefore, it can reveal nonintuitive and nonobvious outcomes that can help in management decisions. The intellectual roots of assessing viability of wildlife populations date to at least the 1930s (Reed et al. 1998*b*). Leopold (1933:47) noted the importance for wildlife managers to recognize "**the minimum number** of individuals which may successfully exist as a detached population."

A subset of viability assessment procedures includes **Population Viability Analysis** (PVA). As the quantitative arm of the body of approaches to assessing viability, PVA can be defined as "the application of data and models to estimate probabilities that a population will persist for specified times into the future (and to provide insights into factors that constitute the biggest threats)" (Mills 2007:254).

We believe PVA embraces the concept of a "**Minimum Viable Population** (MVP)" and makes this concept somewhat obsolete. MVP is problematic for both philosophic and scientific reasons. Philosophically, it strikes us as risky to manage for the "minimum" number of individuals that could persist on this planet. Scientifically, the problem is that we cannot specify a specific "**minimum number**" of individuals that will insure long-term viability, because of all the uncertainties involved in the persistence of a small population.

Several reviews of practical applications of PVA are available (e.g., Sjögren-Gulve and Ebenhard 2000, Young and Clarke 2000, Beissinger and McCullough 2002, Morris and Doak 2002, Reed et al. 2002). We highlight these applications for management of small populations, focusing both on the quantitative framework of PVA, as well as on other methods that constitute the assessment of viability.

Three Characteristics of Population Viability Analysis

Quantitative viability assessment using PVA has 3 central concepts: persistence threshold, time, and likelihood. **Persistence** is usually in the sense of "not extinct," implying that a population remains above zero individuals (or one mating pair). This is an important threshold, but there are often thresholds other than zero that are useful to track for biological or management reasons. These "**quasi-extinction**" thresholds might include, for example, biological thresholds below which Allee effects occur or where strongly interacting species become unable to perform critical ecosystem functions (Conner 1988, Soulé et al. 2003). Quasi-extinction thresholds also may include management thresholds such as the triggering number to bring a wild population into captivity, or the abundance below which a threatened species would be reclassified as endangered (Ginzburg et al. 1990, Burgman et al. 1993, Scott et al. 1995). Therefore, when we refer to "**extinction**" we include both true extinction and quasi-extinction thresholds.

Box 35.3. COMPONENTS OF A POPULATION VIABILITY RISK-MANAGEMENT PROCESS

1. *Describe the species.* Identify and screen for species at risk.
2. *Describe pertinent regulations and laws.* Define the range of acceptable conditions that meet policy regulations or law. Identify responsible agencies and institutions and coordinate their planning activities.
3. *Describe species' conditions and ecology.* Describe the species' environmental relationships and reasons for viability concern or population decline.
4. *Develop planning alternatives.* Develop a range of planning or management strategies. Describe risk attitudes of publics and responsible agencies and institutions. Describe perceived and expected utilities of planning alternatives. Identify factors and value ranges in decision criteria to be used to select among the alternatives.
5. *Evaluate viability effects of the alternatives.* Conduct a viability risk analysis. Analyze how the alternatives affect population size, distribution, and persistence, resource tradeoffs, and social concerns.
6. *Array the alternatives according to anticipated effects.* Assess the benefits to population viability, indirect costs, opportunity costs, and foregone options for each alternative. Identify and array the range of acceptable alternatives that meet decision criteria.
7. *Select an alternative.* Apply decision criteria to results and select a course of action.
8. *Implement the alternative.* Institutionalize management guidelines of the selected alternative. Develop budgets and track implementation.
9. *Monitor results.* Compile and interpret monitoring information; revisit steps 1–8 as suggested by monitoring information and changing conditions.

From Marcot and Murphy (1996).

A second important component of our PVA definition is **time** (Frankel and Soulé 1981). As with any other prediction (e.g., weather, stock market), the assumptions used in PVA will be less and less reliable further into the future. Scott et al. (1995) proposed that when PVA is used in endangered species recovery plans it should incorporate **short-term projections** that are evaluated over time against a long-term goal (see also Goodman 2002). The **long-term** viability assessment should include goals that are biologically based. The short-term projections should explicitly incorporate political–legal–social constraints; monitoring and the iterative application of short-term PVAs can be used to evaluate how well long-term goals are being achieved. Thus, public review (and political trade-offs) can be incorporated in choosing short-term management strategies, but ultimate success is judged against the yardstick of the long-term, biologically based goal.

The final component of the definition of PVA is "**likelihood.**" Obviously, a higher probability of persistence over a given time will require a larger initial population size. Likelihoods are captured in quantitative PVAs with "**quasi-extinction curves**" (Burgman et al. 1993, Groom and Pascual 1998, Akçakaya 2000). There are many ways likelihoods can be portrayed; they are usually presented as the probability of reaching a quasi-extinction threshold over a range of time, or the probability of reaching different population sizes at some point over a fixed time, or the risk of decline by a given amount. Consideration of these PVA components (viability threshold, persistence time, and likelihood of persistence) argue for PVA being conducted as an examination of alternatives, with a range of data and products, instead of performing just one PVA for a species with "*X*" data for "*Y*" probability of persistence over "*Z*" years.

Many key aspects of PVA have a strong biological basis, but the selection of goals requires the addition of a **social component.** Issues such as "For how long do we want to evaluate persistence?" and "How secure should that persistence be?" require social, cultural, economic, and political considerations (Shaffer 1987; Tear et al. 1995, 2005; Ludwig and Walters 2002; Svancara et al. 2005).

APPROACHES TO ASSESS VIABILITY

We describe several approaches to assessing viability (Mills 2007). The first 3 methods are quantitative approaches of PVA. The second 2 are alternate methods for assessing viability when data are sparser.

Population Viability Analysis Methods

Time Series

If a series of abundance estimates over time is available for a small population, those data can be used to estimate the probability of reaching quasi-extinction thresholds. The mathematical approaches can become complicated as they attempt to accommodate real-world biological and sampling issues such as density dependence, the ability to sample only one stage of a population (e.g., egg counts, breeding adults), sampling variation, and missing data. Morris and Doak (2002) provide a readable overview of this considerable literature.

Underlying all approaches is the idea that a time series of abundance estimates can be characterized by an average trend and variance in that trend (see Humbert et al. [2009] for the best way to estimate these for exponential growth); if past trends and variability are assumed to be reflective of the future, one can calculate the probability that the population might reach some quasi-extinction threshold in the future. The math captures the nonintuitive, but important, fact discussed earlier that variance in population growth rate means that even populations that tend to increase, on average, may be most likely to decrease to extinction. From a practical viewpoint, this implies that effects of management on variability in population growth can be as important as effects on the growth rate itself (Burgman et al. 1993).

As an alternative to estimating trend and variance, "**risk-based viable population monitoring**" uses a simple exponential growth model to directly estimate risk of decline over time, updating the risk assessment with each new abundance estimate, providing an efficient means of warning of future declines and demonstrating status (Staples et al. 2005). Software is available (http://www.cnr.uidaho.edu/population_ecology) to implement this methodology, building off an exponential growth model that incorporates both process and sample variance (Humbert et al. 2009).

Demographically Explicit Models

This class of PVA models uses estimates of vital rates, including **age- (or stage-) specific survival and reproduction rates,** their variances and covariances, and other information such as age structure and sex ratio of the population, density dependence, and effects of inbreeding depression. Although this method requires difficult-to-obtain information, it has the advantage of assembling biological information in a way that suggests specific actions that might reduce the chance of extinction (Beissinger and Westphal 1998, Mills 2007). For example, for an Amazonian forest frog (*Anomaloglossus stepheni*) declining on Amazonian forest fragments, adult male survival was not reduced by fragmentation, but mean clutch size was reduced by 17%. Biological meaning for these changes came from a demographically explicit model, which showed that a reduction in clutch size of this magnitude would be sufficient to cause the observed magnitude of population declines in fragments (Funk and Mills 2003).

Because of the multiple interacting factors in a demographically explicit PVA, **computer simulations** are typically used. Demographic stochasticity in survival is usually applied in 1 of 2 ways. The first approach draws the number of survivors in a cohort from a **binomial distribution** with the specified mean survival rate for that time step and number of individuals in the cohort. The second way that demographic stochasticity is incorporated is to pick, for each individual, a random number from a **uniform distribution;** if the chosen number is greater than the mean survival rate of that time step, the individual dies; if it is less, the animal lives.

Mean survival (and reproduction) rates change in each time step due to environmental stochasticity. Operation of environmental stochasticity is mimicked in a PVA by choosing mean vital rates for each time step from a distribution of random numbers with a specified mean and variance (the variance is the process variance, separated from sampling variance). An alternate approach may randomly pick one of several vital rates measured in the field (or even entire matrices of vital rates from field data; Akçakaya 2000). When **modeling environmental stochasticity,** it also is important to specify correlation among vital rates and through time for particular rates because it affects both variance in population growth and probability of extinction (Ferson and Burgman 1995, Groom and Pascual 1998). If necessary, PVAs can include catastrophes (the extreme events outside the normal range of environmental stochasticity) by specifying the magnitude and average timing for their occurrence.

Genetic stochasticity, or the consequences of inbreeding due to genetic drift in a small population, is incorporated into demographically explicit PVAs by decreasing vital rates at different levels of inbreeding. It is difficult to measure both inbreeding level and fitness for most wildlife species (Oyler-McCance and Leberg 2005). Thus, in many PVAs, a range of values from other species are used to bracket possible effects; measurements of inbreeding depression have recently emerged for many wildlife populations (Crnokrak and Roff 1999, Keller and Waller 2002). The shape of the curve relating inbreeding to fitness is complex and includes the extent to which cost of inbreeding is or is not "**purged**" over time (Mills and Smouse 1994, Ballou 1997, Lacy 1997, Frankham et al. 2002). The range of inbreeding costs expected for any species, as well as uncertainty in the shape of the curve relating inbreeding to fitness, implies that incorporating genetic stochasticity is the same as with any other uncertain parameter in PVA (for example, dispersal rates, density dependence, breeding structure, etc.). The user should include a range of plausible possibilities, including "worst-case" and "best-case" scenarios.

Density dependence can and should be incorporated into demographically explicit PVAs if field data are sufficient. Unfortunately, density dependence is one of the hardest parameters to estimate in field populations; yet, subtle differences in how it is included in PVA models can drastically affect predictions (Mills et al. 1996). Burgman et al. (1993:163) argue, "It is probably silly to pretend there exists a perfect density-dependence curve in a scattergram of data and tortuously thread some guess at its form." They present an alternate strategy using field data to describe density dependence in a "density vague" manner. The **uncertainty** of parameterizing density dependence, and its effect on PVA projections, has led to the recommendation that PVA models should include at least one set of runs without density dependence, to provide a baseline understanding of extinction risks (Ginzburg et al. 1990, Mills et al. 1996). The real existence of density dependence will affect the interpretation of the products of the model for a particular management scenario (Boyce 1992, Groom and Pascual 1998).

The framework for incorporating factors into a demographically explicit PVA varies widely. In some cases, it is possible to use "**canned**" PVA programs. Two of the most popular are the **matrix-based RAMAS** (Ferson and Akçakaya 1990, Akçakaya 2002) and the **individual-based VORTEX** (Lacy 2000). Examples of species with published PVAs using these 2 programs include Chinese Hainan eld's deer (*Cervus eldi hainanus* or *C. e. siamensis;* Song 1996), Hawaiian stilt (*Himantopus mexicanus knudseni;* Reed et al. 1998*a*), Florida manatee (*Trichechus manatus latirostris;* Marmontel et al. 1997), and Florida scrub jay (*Aphelocoma coerulescens;* Root 1998). In other cases, particular aspects of proposed management options or of the animal's life history lead to development of PVA programs that are more species-specific, such as for African wild dogs (*Lycaon pictus;* Vucetich and Creel 1999), cheetah (*Acinonyx jubatus;* Kelly and Durant 2000), greater sage-grouse (*Centrocercus urophasianus;* Johnson and Braun 1999), and red-cockaded woodpeckers (*Picoides borealis;* Daniels et al. 2000).

Demographically explicit PVAs also allow the user to perform a **sensitivity analysis** to evaluate which life-history components and/or management actions will have the largest effect on population recovery (Fig. 35.3). Sensitivity analysis in the broad sense (reviewed by Mills and Lindberg 2002) includes a variety of approaches, including direct perturbation of vital rates in a model, analytical sensitivity and elasticity calculations, and simulation-based approaches such as life-stage simulation analysis (Wisdom et al. 2000). Regardless of the approach, sensitivity analysis can guide both research and management. For example, field research into causes of global amphibian declines would be more efficient if coupled with sensitivity analysis to indicate which changes in certain vital rates would most affect population growth rate (Biek et al. 2002). Citta and Mills (1999) showed that sensitivity analysis could be used to explore how to decrease pest population growth by examining options for controlling brown-headed cowbirds (*Molothrus ater*) that would cause cowbird populations to decline. Similarly, sensitivity analysis can be used to explicitly incorporate human demographic, economic, and social systems with PVA of wildlife species (Lacy and Miller 2002).

The main obstacle to using demographically explicit PVA approaches is that they require substantial data. If data are not available, managers should resist the temptation to guess and, instead, should focus on collecting the relevant information or choose a different approach. However, where the match between model needs and data availability are reasonable, a useful approach is to "embrace uncertainty" about processes or parameters by acknowledging the uncertainty explicitly, and considering scenarios across a range of plausible values.

PVA with Multiple Populations

Any PVA approach for a single population can be scaled up from single population analysis to consider multiple populations across the landscape. With sufficient data, multiple-population PVA models can be spatially explicit, incorporating exact spatial locations of populations or individuals or

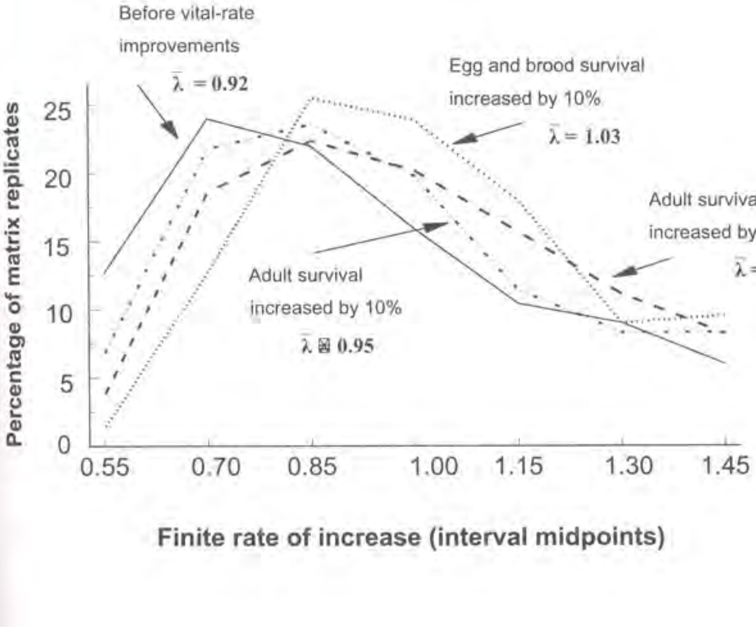

Fig. 35.3. An example of sensitivity analysis using Life-Stage Simulation Analysis (LSA) for greater prairie-chickens. Different potential management actions vary in how successful they would be in modifying the population growth rate. *From Wisdom et al. (2000).*

other features (Reed et al. 2002). Two additional concepts that enter into PVA evaluation of multiple small populations are the extent of **connectivity and correlation** in dynamics among the populations. Connectivity is important because it can lead to gene flow, which affects genetic structure (Mills and Allendorf 1996). It also can facilitate **colonization or recolonization** of unoccupied patches (Singer et al. 2000) and decrease local extinction probability via a "rescue effect" (Brown and Kodric-Brown 1977). Connectivity can, at times, have negative ramifications for small populations across a landscape, as when diseases are transmitted (Cunningham 1996) or maladaptive learned traits are transferred socially (Laland and Williams 1998). **Connectivity** involves complex behavioral processes such as dispersal (Reed et al. 2002), which have traditionally been difficult to measure accurately. However, measurement of connectivity for wildlife populations is becoming easier with development of field and analytical tools based on telemetry, mark–recapture analysis, and genetic sampling (Mills et al. 2003).

The other important component of multiple population models is the extent of correlation in dynamics of different populations. If there is **decoupling** of environmental stochasticity among small populations, it becomes much less likely that a single bad year or series of years would cause all populations to be lost (Harrison and Quinn 1989). For example, consider 3 populations of 50 animals each. If all 3 populations had probabilities of extinction of 0.2/year, but their probabilities were independent (because of decoupling of environmental stochasticity), the probability of total extinction for all 3 populations in a given year would be $(0.2^3) = 0.008$. In contrast, if the fates of the populations were completely coupled (for example, the populations were adjacent to each other), the probability of total extinction would be 0.2/year, the same as for 1 population.

The extent of **correlation, or coupling,** in environmental stochasticity can be largely affected by distance among populations, because similar climatic events or other perturbations (invasions by exotics, deaths caused by predators or disease, etc.) are more likely to occur simultaneously to populations that are close together. Movement of individuals (connectivity) also facilitates correlations among population. For example, Canada lynx (*Lynx canadensis*) populations across western North America are connected by dispersal, which may facilitate the relatively synchronous dynamics of lynx populations at the continent-wide scale (Schwartz et al. 2002).

In addition to application of time-series or demographically explicit models across more than one population, data for species with multiple populations facilitates another type of PVA. These are broadly called "**patch occupancy models,**" or "incidence function models" (Hanski and Ovaskainen 2000, Hanski 2002). They are conceptually similar to logistic regression modeling of colonization and extinction events (e.g., Sjögren-Gulve and Ray 1996, Sjögren-Gulve and Hanski 2000). Focusing on the widely used incidence function models, the key data are patch occupancies (whether or not a patch is occupied). The other parameters are **distance** between patches (metrics of connectivity other than distance can be used if available) and **size** of the patches ("size" can be scaled to account for habitat quality, but population size is ignored, and patches are assumed to be distinct). An important assumption of incidence function models is no increasing or decreasing trend in patch occupancy, for example due to recent severe habitat loss (Moilanen 1999, 2000). **Incidence function models** are best suited for short-term predictions of consequences of management scenarios rather than predicting long-term extinction risk. They are most appropriately used for relatively common species with rapid turnover of local populations in fragmented landscapes (Hanski 2002). If populations are relatively large or long-lived, so that local (within-population) dynamics are important, then other approaches are more appropriate (e.g., Lindenmayer et al. 1995).

Other Approaches to Assess Viability

From a biological perspective, the worst-case scenario is conducting an assessment of viability when time is short and data are scarce to nonexistent. Yet, this is normal for wildlife biologists around the world when adequate data for time-series, demographically explicit, or multiple population models are lacking. For example, in 1993, the President of the United States appointed a Forest Ecosystem Management Assessment Team (FEMAT) to evaluate the effects of large-scale timber-harvest options on wildlife species in western Washington, Oregon, and northern California (Forest Ecosystem Management Assessment Team 1993, Meslow et al. 1994, Thomas 1994). More than 1,000 plant and animal species were to be included in the assessment, including many species that were (and are) little known. The team had 3 months to complete the job. Difficult, if not impossible, tasks such as this are given to biologists far too often, and the problem is exacerbated on the global scale where data are often even sparser.

In the case of the 1,000 species assessed as part of FEMAT, the best that could be done was to implement a subjective "**expert panel**" approach to assess viability. This method had evolved from earlier use in analyses in the Pacific Northwest of the United States (e.g., Thomas et al. 1993), and continued to evolve after the FEMAT process (Marcot et al. 1997).

Unfortunately, whenever expert opinion or other subjective approaches are the only options for assessing viability, the results will be somewhat suspect. Humans are inherently bad at guessing risks (even when they are informed guesses), in part because we are led astray by factors such as how visible or controllable the risk appears, or the consequences of the risks (Burgman et al. 1993). Thus, we overestimate many low-level risks (e.g., death by tornado) and underestimate high-level risks (e.g., death by heart disease). Second, and perhaps more importantly, the subjective decision-making process is based on the experience of the "expert" making the decision; "severe risk" will mean different things to different people. It is difficult to make transparent or testable the logic, mechanisms, predictor variables, sources of uncertainty, or other processes that go into the outcome of an expert judgment. Expert opinion assessments of viability will remain an uncomfortable and insufficient last resort.

In closing the discussion of methods for assessing viability, it is important to consider less data-intensive methods that are not part of PVA per se, but which can be used to assess viability when detailed population data are not available. Two approaches are described.

Rules-of-Thumb

Rule-of-thumb approaches assign qualitative ranks of risk using specified, operational criteria (reviewed by O'Grady [2002]). Common rule-of-thumb approaches include those developed by The Nature Conservancy (Master 1991, Master et al. 2000, Samson 2002) and the World Conservation Union (IUCN) Red List Categorization System (Mace 1995, IUCN 2001, Mace et al. 2008).

As an example of a rule-of-thumb approach, we focus on the IUCN Red List Categorization System (Mace and Lande 1991; Mace 1994, 1995; Gärdenfors 2000; IUCN 2001), which forms the basis for "Red Lists" that assess the conservation status of >18,000 plant and animal species worldwide.

Specifically, the IUCN approach (see Table 35.1) assigns species to 1 of 9 categories. To be placed in 1 of the 3 **categories at risk of extinction** (i.e., critically endangered, endangered, and vulnerable), at least one operational rule-of-thumb criterion must apply. These **criteria include** (1) rapid population decline, (2) small geographic range and decline, (3) small population size and decline, (4) very small or restricted population size, and (5) unfavorable quantitative analysis (Mace et al. 2008; Fig. 35.4). The fifth criterion for assigning species (quantitative analysis) includes a direct quantitative estimate of extinction probability within specified timeframes using a PVA. However, data limitations mean that, in practice, the IUCN system usually consists of criteria 1 through 5 (Mace and Lande 1991, Gärdenfors 2000). Sophisticated methods for making uncertainty explicit in the risk assessment procedure have been proposed for IUCN categorization (Todd and Burgman 1998, Akçakaya et al. 2000, Taylor et al. 2002), and software is available to standardize the process (Akçakaya and Root 2007).

A key philosophy behind the IUCN approach underscores an important general point about small population management; a distinction is made between assessing the severity of threat and setting conservation priorities (Mace 1994, 1995; Gärdenfors et al. 2001). Categories of threat established by the rules-of-thumb are just one piece of information used to set conservation priorities. At least as important are additional criteria, which might include likelihood of success in restoring the species, number of other threatened species occupying the same habitat, taxonomic uniqueness, availability of funds, and the legal and political framework for conserving a particular species.

There are obvious **limitations** to any rule-of-thumb approach. For example, a single set of rules will not fit all species and situations (O'Grady 2002). Despite the limitations, biologists must turn to these methods at times, because they may be the best available. Mace and Hudson (1999:244) reported that

> Although the IUCN system may be efficient at picking up different species facing diverse threats, it is not designed to be an accurate tool for measuring extinction risk, for projecting population status, or for designing population management plans. Its role is to highlight species exhibiting one of several symptoms of pending extinction and to classify species according to the relative severity of the apparent threat. The **Red List** is a useful conservation tool only when listing leads to measures to assess the causes of threat and to develop, where necessary, appropriate management responses and species recovery plans. In short, the IUCN red list criteria are designed to be robust and precautionary across a wide range of circumstances, to operate when data are scarce, and to pinpoint species in need of attention.

In contrast to the IUCN guidelines, the **Endangered Species Act** of the United States does not offer specific rules-of-thumb criteria for identifying species at risk of extinction. The ESA **uses qualitative assessments** to classify species as **endangered** ("in danger of extinction throughout all or a significant portion of its range"; USFWS 1973:2) or **threatened** ("likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range"; USFWS 1973:4). Classification, or listing, is based "solely on the basis of the best scientific and commercial data available . . . after conducting a review of the status of the species" (USFWS 1973:5). In the absence of robust criteria for listing and recovery, **listing determinations and recovery goals** have often been inconsistently applied (Scott et al. 1995, Tear et al. 1995).

Approaches Based on Habitat and Other Information

At times, more information is available about species–habitat relationships than demographic variables for a **species of concern.** Although we believe that the relevant population data should be collected for a proper viability assessment, there are cases where habitat information alone can contribute useful information (Boyce 1992). Recently, researchers in federal land-management agencies in the United States have developed a **Bayesian Belief Network** approach that

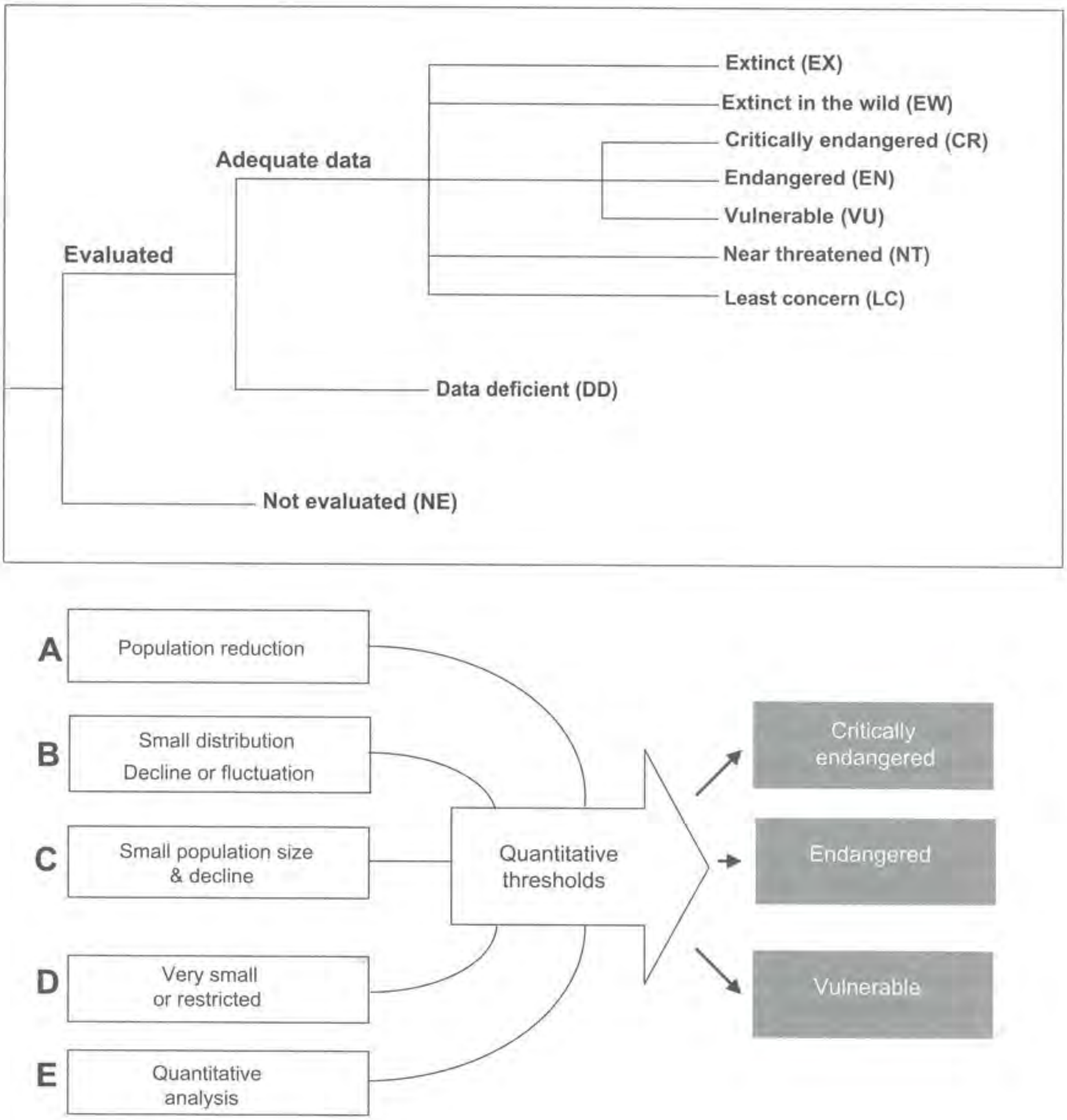

Fig. 35.4. The International Union for the Conservation of Nature (IUCN) population assessment procedures. *From Gärdenfors et al. (2001), IUCN (2001).*

combines vegetation associations with other information for region-wide or species-wide assessments (Lee 2000, Marcot et al. 2001, Raphael et al. 2001). Information in the Bayesian Belief Network includes associations with habitat and other variables, as well as expert opinion and ancillary models (including true PVA models). When expert opinion is included, it is incorporated so it can be easily scrutinized. Using a Bayesian statistical framework, input variable values are combined with conditional probability tables to estimate the probability of a response relevant to population status. Risks associated with alternative courses of actions can be explored. As an example of this approach, 28 species have recently been assessed as part of land planning for the 58-million-ha Interior Columbia River Basin (for example, Wisdom et al. [2002] for assessment of greater sage-grouse and Rowland et al. [2003] for wolverine).

Marcot et al. (2001:29–30) described the **utility and limitations** of these approaches, noting that they do not substitute for the more rigorous and quantitative PVA approaches. Rather, these approaches are most useful when empirical data on demography and genetics are unavailable, but a decision-making process is inevitable. In these cases "the experts must provide their best professional evaluation or step aside and let activities proceed."

PRACTICAL THOUGHTS ABOUT WILDLIFE RISK ASSESSMENT

The largest benefit to assessing viability for a small population is that it forces us to be explicit about the threats to a population. It places assumptions on the table where they can be discussed. For example, if one person believes that genetic isolation is the largest threat for a particular species, they may argue that connectivity enhances viability; alternatively, someone else concerned about disease risk for that species might argue that connectivity decreases viability. The assumptions are explicit.

From published works and our own experience, we offer 3 important messages regarding **assessing viability** as part of the management of small populations. First, be aware of the **quality of data** available and match those data with the most appropriate approach. Currently there is interest in the effects of data quality and sampling error on model performance. **Sampling error** will tend to make nature seem more "variable," which tends to bias upward the predicted probability of extinction. The extent to which sampling error compromises PVA has been discussed intensely (Ludwig 1999, Fieberg and Ellner 2000, Meir and Fagan 2000, Holmes 2001, Sæther and Engen 2002). In any case, wildlife biologists should heed suggestions on how parameters of viability models can be estimated so that sampling error can be quantified (White 2000*b*, White et al. 2002). Second, viability assessment is more useful as a **comparative tool** for ranking management options than it is for making precise predictions of viability. Although there can be heartening matches between PVA predictions and actual population trajectories (Brook et al. 2000), instances where this is true are likely limited (Lindenmayer et al. 2000, Coulson et al. 2001).

Using PVA to evaluate relative merits of different management options allows it to be incorporated into the decision-making process that guides management action and policy (Maguire 1991, Noon and McKelvey 1996, Dreschsler and Burgman 2004). For example, consider a case of how PVA was used to improve the decision-making process (Fig. 35.5). Management of the Australian marsupial, **Leadbeater's possum** (*Gymnobelideus leadbeateri*), is one of the most contentious forestry issues in Australia. The primary threat to this species is its requirement for nest sites in trees >150 years old. Early this century, fires burned >60% of the forest within the range of the species, and clearcut logging has more recently occurred over 75% of its known distribution. The species now occupies an area 60 km <00Δ7> 50 km in the central highlands of the state of Victoria in southeastern Australia. Current management is to avoid cutting in certain areas (including old-growth patches) while clearcutting continues in other areas; areas that burn in the future may be salvage-logged.

Possingham et al. (2002) examined the viability of Leadbeater's possum subject to current and potential future management options (see Fig. 35.5). Under current management, possums would be expected to persist for the next 150 years (only 38% chance of extinction), but not into the future (100% chance of extinction). If old-growth forest was not salvage-logged, trees damaged (but alive) after a fire would not be removed; this would increase possum viability so that extinction probability would decrease to 33% and 58% over the next 150 years and expected long term, respectively. If there were further limitations to **salvage logging,** so that it was prohibited both in old growth and in other areas that could grow into old growth, extinction probability drops even more. Two popular suggestions for further aiding this species are to increase the rotation time and to make more reserves, so these possibilities were considered next. Although increasing rotation time decreases extinction probabilities, it requires an almost complete halt of logging for the next 150 years, hardly a politically realistic possibility! In contrast, setting aside **reserves** improves viability even more, but reduces logging little; for example, setting aside just 6 (50-ha) reserves (5% of the forest block) decreases extinction probability to 18% over the long term, but reduces logging by only 5% at most. With identification of additional permanent reserves as a viable approach, a number of scenarios were considered, trading size and number of reserves. The authors **assessed the sensitivity of conclusions** by modeling a range of possibilities for processes about which they were uncertain. The recommendations emerging from this work are currently being implemented (Possingham et al. 2002).

Clearly, PVA needs to be explicitly and seamlessly incorporated into a small-population modeling and decision-making process, analogous to the **adaptive management framework** used to marry field data, biological process, sociopolitical goals, and management strategies for harvested species. Incorporating PVA as part of such an adaptive management framework for small populations has been termed **Population Viability Management** (PVM; Bakker and Doak 2009). As an example for endangered island fox (*Urocyon littoralis*) on the Channel Islands (Bakker and Doak 2009), the first step is to set recovery criteria in terms of quasi-extinction risk in a public forum, accounting for the inevitably complex sociopolitical and biological considerations. Next, readily monitored population attributes are chosen (adult population size and adult mortality in this case), and PVA is used to link these attributes to quasi-extinction thresholds, clarifying that uncertainty in the monitoring data will delay the delisting of a recovering population (Fig. 35.6). Finally, PVM incorporates management actions that will affect the population attributes; for example, determining how decreasing predation on fox by controlling golden eagles (*Aquila chrysaetos*) would achieve delisting, given the practi-

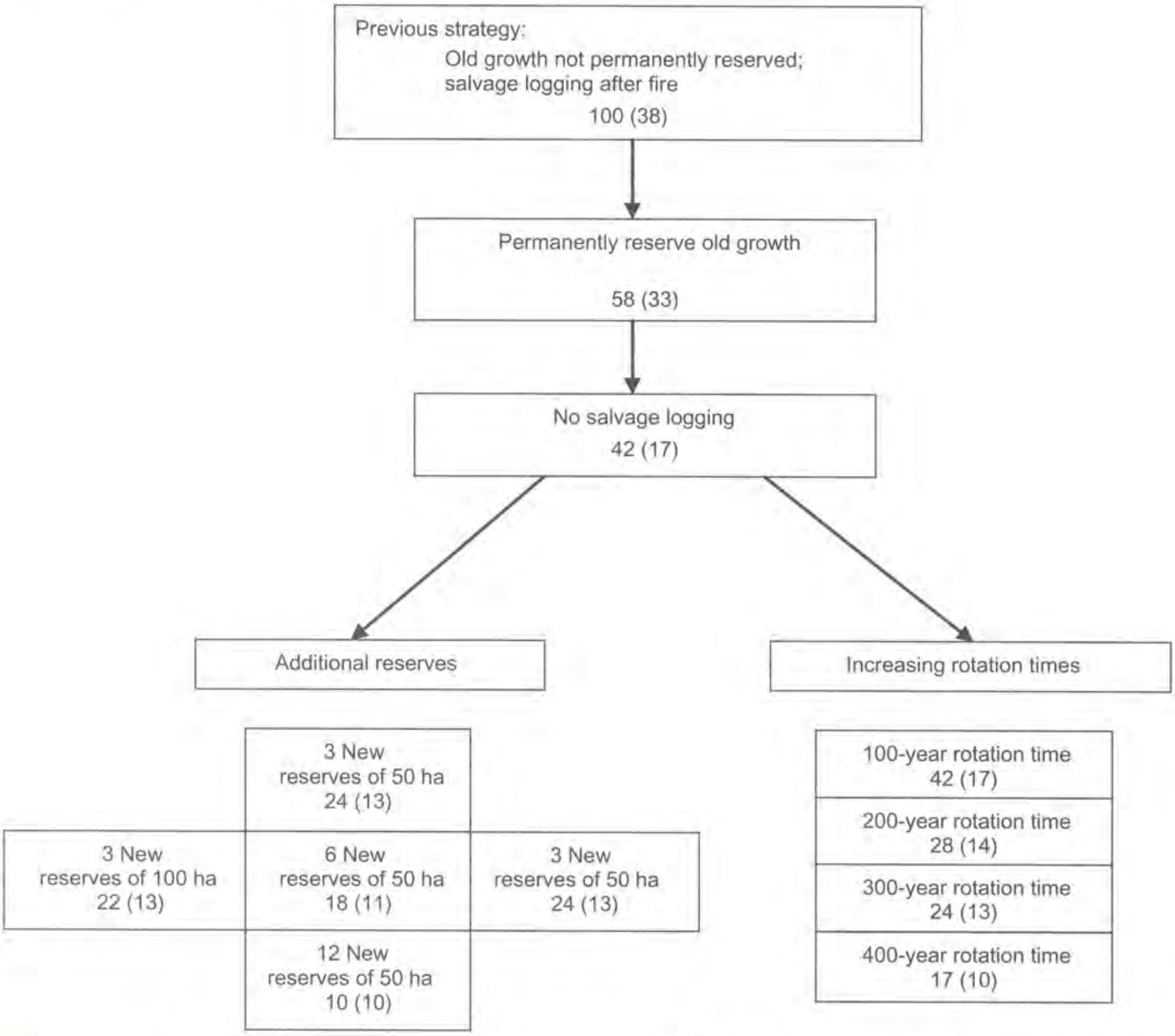

Fig. 35.5. Population viability analysis for decision analysis, made in the case of Leadbeater's possum. For each option, the number gives the probability of extinction over the next 150 years (in parentheses) and over a typical 150-year period in the future when the forest has reached equilibrium with the management actions (think of this as the period 500–650 yr from now, assuming constant conditions). *From Possingham et al. (2002).*

cal constraints of monitoring. As with the possum example, we see that PVM provides a platform for integrated adaptive decision-making. This would allow increasing knowledge and changing management outcomes to be accounted for in data-based decisions.

A third message for assessing viability is to **consider a range of possibilities** for every step of a PVA for which there is doubt about a process, functional relationship, or measured parameter. The worst PVAs are those that take one set of data and provide one estimate of extinction probabilities, while the best are those that consider a variety of biological and management information to produce a range of predictions (Taylor 1995, Ellner et al. 2002). Ideally, a PVA would be performed with multiple methods (Mills et al. 1996, Gärdenfors 2000, Kindvall 2000). **Sensitivity analysis** in the broad sense, evaluating how information affects products, is an essential part of PVA (Reed et al. 1998*b*, Mills and Lindberg 2002). Also, Bayesian approaches directly incorporate parameter uncertainty into analysis (Taylor et al. 1996, 2002; Goodman 2002; Wade 2002).

Burgman and Possingham (2000:104) recalled the comment that "**All models are wrong, but some are useful**" (from Box 1979) to emphasize their point

> The only correct model is an entire reconstruction of the actual system—whereupon it ceases to be a model. The utility of a PVA is determined by several things, including the care taken to include all ecological intuition faithfully, the care taken to represent all views (hypotheses) as structural alternatives, the detail and transparency of state-

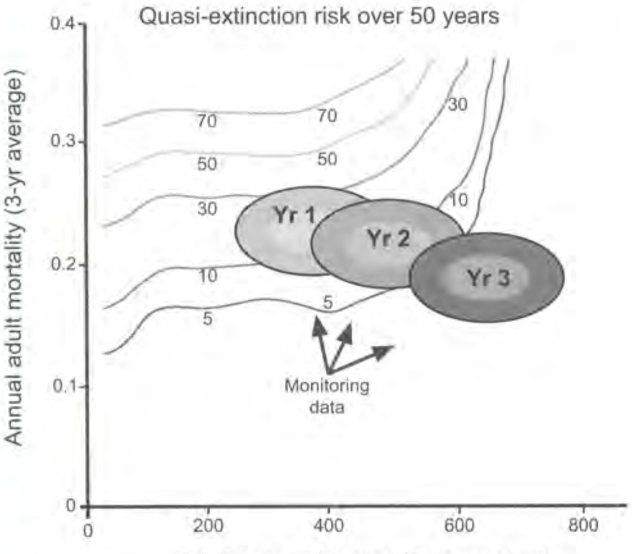

Fig. 35.6. An example of Population Viability Management (PVM) as an adaptive management strategy for endangered island foxes on Santa Cruz Island. The consensus recovery criteria was a 5% risk of quasi-extinction over 50 years (dark blue isocline in figure), with uncertainty in monitoring data controlled for by requiring that 80% confidence regions fall below the risk isocline. Different management actions that affect vital rates (e.g., predator control, captive breeding) can be compared via PVM, recognizing that less precise monitoring data (outer region of monitoring data ovals) could delay meeting the delisting criterion (because less of the confidence region would fall below the risk isocline). *From Bakker and Doak (2009).*

ments about assumptions, and the role of the model within the decision-making framework. One of the most important steps in establishing the credibility of a PVA is to communicate the uncertainties embedded in the model and its assumptions.

MANAGEMENT OF SMALL POPULATIONS

The results of a viability assessment or sensitivity analysis can provide managers with specific insights into how to most effectively increase size of a small population and reduce risk of extinction. A variety of techniques can be used; some are identical to those used with abundant species, but many others are especially adapted to the needs of populations with small numbers of individuals.

Effective management of small populations must address both **ultimate and proximate causes** of population declines. The ultimate cause of a species' decline is usually some change in the environment resulting from human activities. These changes might be novel events the species has not experienced (e.g., introduction of synthetic toxic chemicals, like DDT, into a species' food chain) or somewhat normal events that suddenly occur in **temporal or spatial patterns** that are unprecedented (e.g., disturbing a forest through logging more frequently and on a different spatial scale than would occur under natural disturbance regimes, thus eliminating old-growth conditions). Regardless of the ultimate cause, the population fails to cope, resulting in proximate causes of decline such as reduced survival and reproduction, or both. Species are often faced with multiple threats whose effects are poorly documented; therefore, it is often difficult to distinguish between proximate and ultimate threats (Gurevitch and Padilla 2004).

The distinction between ultimate and proximate causes of species declines can lead to a dichotomy in management approaches (Temple 1978*b*). Clearly, management must correct the **ultimate causes** of decline by addressing the specific environmental changes that threaten the small population. **These causes include** such widespread problems as habitat loss or deterioration, effects of exotic organisms, toxic chemicals, and mortality directly related to human activities. Frequently, ultimate problems are difficult to remedy; typically, a long time is required for corrective measures to improve a species' environment. Time is a factor working against the persistence of most small populations.

To hasten recovery of a perilously small population, managers often must address **proximate factors** in a manner that is somewhat unrelated to the ultimate cause of a population's decline. Typically, the approach is to increase **survival and reproductive rates** by whatever means possible to stimulate population growth (ideally, building on the efficiencies made possible by sensitivity analysis; see next section). Ultimate problems are then addressed somewhat independently of these activities, which is similar to the treatment of a critically ill patient in a hospital's emergency room: treat the life-threatening symptoms and then remedy underlying problems (Zimmerman 1975).

Two birds, **osprey** (*Pandion haliaetus*) and **peregrine falcon** (*Falco peregrinus*), illustrate the benefits of addressing proximate problems (Spitzer 1978, Cade et al. 1988). Both species were threatened by the ultimate problem of contamination of their food chains with **chlorinated hydrocarbons,** especially dichlorodiphenyltrichloroethane (DDT). In each situation, populations declined precipitously after reproduction was impaired when eggs with DDT-thinned shells failed to hatch. Although measures were taken during the late 1960s and early 1970s to address the ultimate problem, by curtailing use of the offending toxic chemicals, both species continued to decline and remained at risk because of the persistence of the chemicals already in the environment.

To offset the proximate problem of inadequate recruitment, managers successfully augmented reproduction in wild ospreys and **released captive-reared individuals** into wild populations of peregrine falcons. Reproduction of ospreys was enhanced by reducing nest-site limitations through **erecting artificial nest platforms** in areas that lacked natural nesting sites (Postupalsky 1978), and by replacing thinshelled eggs with thick-shelled eggs (Spitzer 1978). Captive breeding and subsequent reintroduction of peregrine falcons provided an important boost to recruitment to populations that were producing too few young (Cade et al. 1988), which was critical to achieving positive population growth (Kauffman et al. 2003). In both situations, regional populations were doomed to eventual extinction unless attention to proximate causes improved the status of the species while ultimate problems were being addressed. In the post-DDT era, both ospreys and peregrine falcons recovered impressively after chlorinated hydrocarbon pesticides eventually were purged from the food chain (Spitzer et al. 1983, Cade et al. 1988).

The **efficacy of specific management actions** affecting particular vital rates can be assessed using sensitivity analysis. Next, we describe the critical links necessary to efficiently connect management actions to specific vital rate changes and increases in population size of small populations.

Improving Birth and Death Rates

The fundamental truth most relevant to managing small populations is that management actions are not all equal in influencing birth and death rates, and all birth and death rates are not equal in how they influence population growth (Mills 2007). The key, then, is to identify which management actions, through their effects on vital rates, will be most efficient at achieving an increase in numbers for small populations.

The good news is that an impressive toolbox of analytical approaches exists to quantify how individual birth and death rates alter population growth (see "Demographically Explicit Models" section above). Some vital rates have particularly large proportionate or absolute influence on population growth even though they vary relatively little, while others affect population growth because they can be changed drastically in nature or under management (Mills et al. 1999).

In some cases, enough work has been done to generalize across taxa which vital rates are most "important" for increasing population growth. For example, in ungulates and indeed across many long-lived species, **adult survival** tends to have the highest proportionate effect on population growth, but **calf survival** tends to vary so much that it is often the vital rate that most drives variation in population growth (Gaillard et al. 1998, Raithel et al. 2007). For endangered Sierra Nevada bighorn sheep (*O. canadensis sierrae*), life-stage simulation analyses indicated that, indeed, adult survival had the highest proportional effect on population growth; however, different populations differed in which vital rate had been disturbed the most, so that the most **"important" vital rate,** and most effective management strategy (e.g., predator control or augmentation), was population-specific (Johnson et al. 2010). A critical information need is to determine how different management actions affect vital rates in small population, thus connecting the dots between management actions, vital rates, and population growth rate.

With demographic models guiding the process of identifying **proximate vital rates** that will most efficiently change population growth rate, the manager will be poised to implement management to improve those rates. Methods exist to increase both reproduction and survival. In birds, **natality** (e.g., litter size or clutch size) can be increased by stimulating additional egg laying bouts via removal of eggs from the nest. **Egg viability** can be ensured by artificially incubating the extra eggs or placing them in nests of foster parents (Cade 1978). A few species present the opportunity to increase frequency of reproduction. Animals that have long periods of **parental care** of offspring are inhibited from reproducing while caring for dependent young. Shortening the time to independence can reduce the intervals between breeding. For example, California condors (*Gymnogyps californianus*) can be induced to breed annually, in contrast to the normal biennial rate, thus effectively doubling fecundity (Snyder and Hamber 1985).

In some populations, only a proportion of the reproductively competent individuals have the **opportunity to breed. Shortages of specific resources** essential for breeding typically are responsible for limiting the number of breeders in a population. If these limitations to breeding can be removed, previously excluded individuals can breed. **Nesting sites** frequently limit the number of breeders and provision of artificial nesting sites such as nest boxes, cavities, and burrows can result in improved fecundity (Snyder 1978).

Reproductive failures normally reduce recruitment below the potential rate suggested by a species' natality. Losses of young before recruitment into the population can be substantial. Preventing those losses effectively increases recruitment. Many techniques have been used, including the quality of breeding sites, reducing risks (e.g., predation) to young animals, or implementing **"head starting"** approaches that give young animals improved prospects for survival to breeding age (Temple 1978*b*).

Survival also may be increased as a means of stimulating population growth. **Reducing effects** of predators, pathogens, competitors, and accidents can be effective (Jackson 1978). These manipulations may reduce losses below normally expected levels and enhance survival in a population, even if poor survival is not an important factor in the population's decline. For example, protecting an endangered species from human exploitation can improve survival, even if overexploitation is not an identified cause of endangerment. **Improving the quality of a species' habitat** also can improve survival; however, habitat improvement is rarely a short-term solution.

Population Augmentation

Translocations can be used for augmenting small populations to increase population size, enhance genetic diversity, diversify age or gender composition, or create new populations through reintroduction to a previously occupied area. Examples include amphibians (Arano et al. 1995, Marsh and Trenham 2001, Rathbun and Schneider 2001; but see Seigel and Dodd 2002 and Trenham and Marsh 2002), adders (*Vipera berus;* Madsen et al. 1996, 1999), greater prairie-chickens (Soulé and Mills 1998), red-cockaded woodpeckers (Allen et al. 1993, Haig et al. 1993, Carrie et al. 1999), Laysan ducks (Reynolds et al. 2008), New Zealand robins (*Petroica australis;* Armstrong and Ewen 2002), sea otters (*Enhydra lutris;* Bodkin et al. 1999), cougars (*Puma concolor;* Ruth et al. 1998), black bears (*Ursus americanus;* Eastridge and Clark 2001), and woodland caribou (*Rangifer tarandus caribou;* Compton et al. 1995). In spite of some high-profile successes, Griffith et al. (1989) and Wolf et al. (1996) found that only about two-thirds of translocations in the United States, Canada, Australia, and New Zealand were considered successful, with success rates varying among taxonomic groups. Drake and Temple (Chapter 36, This Volume) provide a thorough discussion of guidelines, issues, and techniques related to animal translocation.

Habitat Protection

When populations are small because of the **ultimate problem of habitat loss or fragmentation,** protection or restoration of habitat is a necessary step in preventing further declines and increasing population size. Recovery of populations to sizes that are robust to stochastic factors will not occur unless larger habitat patches are available to support a viable population size. A PVA can provide managers with an estimate of the habitat requirements (quantitatively and qualitatively) for a viable population and goals for habitat protection and restoration. For example, spatially explicit PVA models examined how proposed habitat management actions in a U.S. Forest Service District would affect Bachman's sparrows (*Aimophila aestivalis*), a species endemic to pine woodlands of the southeastern United States (Liu et al. 1995).

We live in an increasingly fragmented world; therefore, nearly all **protected areas** (e.g., National Wildlife Refuges, National Parks, wilderness areas, private nature reserves, wildlife management areas) are small and increasingly embedded in substrates that prevent distant movements of many of the species for which protected areas were established. Newmark (1987, 1995) found that in western North American parks, extinctions have exceeded colonizations since park establishment and that rate of extinction was inversely related to park area.

DellaSala et al. (2001) found 97% of all protected areas in North America to be 10,000 ha in size, with 76% of all reserves 200 ha. By themselves, these areas are **too small to support viable populations** of even small animals, and far short of the area needed to support larger carnivores or ungulates (Schonewald-Cox 1983). When reserve sizes were compared to the minimum area requirements of terrestrial mammals in eastern North America (Gurd et al. 2001), only 14 of 2,355 existing reserves (0.6%) were sufficiently large to meet the lower confidence limit of the area required to prevent loss of terrestrial mammal species. This analysis may be optimistic for species conservation, because use of the upper confidence limit rather than the lower would mandate even larger reserves for maintaining viable populations of mammals.

Collectively, these findings of the inadequacy of protected areas mean, first, that management of the **matrix surrounding protected areas** is essential; and second, that even after important habitat areas are identified for protection, it is frequently necessary to plan for ecological restoration (a long-term process) to create habitat in areas not presently suitable for the species (Howell 1988). In addition to occurring in only a fraction of the species' **historical range,** many small declining populations occur at the extremes of former range in habitats that may be suboptimal. The whooping crane (*Grus americana*) provides an example (Lewis 1986), as do many of the upland forest birds of Hawaii (Scott et al. 1986, Channell and Lomolino 2000). **Habitat restoration** may be essential to allow a small population to expand its size to the point that it can be considered no longer in danger of extirpation.

Monitoring

Establishing **monitoring programs** for small populations presents special challenges for the manager. At the most fundamental level, the range of a rare species and its specific habitat requirements may not be known. **Surveys,** thus, may be conducted in unused or unsuitable habitat, unnecessarily increasing the cost of monitoring efforts. Also, observers may be unfamiliar with identification of a rare species and, after failing to find it, conclude incorrectly the population has been extirpated (Scott et al. 1986, Diamond 1987, Reed 1996), or underestimate the effort needed to detect individuals and delineate the limits of small populations (Scott et al. 2008). Finally, small populations will inherently have statistical limitations of insufficient power to detect trends.

Ideally, a monitoring program should address these issues by incorporating as much information as possible about the species' putative range and its habitat associations within that range. It should include a **species-specific program** to train observers in survey techniques and accurate identification of the species of interest, including exposure to the full range of variation (e.g., plumage, pelage, vocalizations, or sign) for the species (Kepler and Scott 1981, Scott et al. 1986). To infer the presence or absence of the species, an important component of the monitoring program will be estimation of the probability of detecting the species at a particular point (Reed 1996, MacKenzie et al. 2002). **Detection** is dependent on a variety of factors (Kepler and Scott 1981, Scott et al. 1986, Reed 1996) including density of individuals, sampling effort, species behavioral characteristics, observer bias, weather conditions, time of day, season, and ambient noise (e.g., wind, water, or anthropogenic noise). **Noninvasive genetic sampling** (Box 35.4) has particular promise (although

Box 35.4. The National Lynx Survey and ethics in collecting data on small populations

For many small populations, the first step in monitoring requires an inventory to identify where the species exists. In the lower 48 United States, the Canada lynx became a species of special concern to land managers in the late 1990s, and was listed in March 2000 as a federally threatened species. However, it was not known precisely where the species occurred in its range in the continental United States. The National Lynx Survey was conceived to bring the properties of consistency, standardization, and reliability to the process of identifying current range for lynx, thereby providing a basis for subsequent monitoring.

The National Lynx Survey sampled lynx distribution at an unprecedented scale: 16 states across the northern United States. Collection of samples required the efforts of hundreds of field personnel. The sampling device for this elusive and low-density species was noninvasive, based on 10 × 10-cm carpet pads smothered in a beaver castoreum and catnip oil scent lure, with nails sticking out. Lynx (and other species) willingly rub against it and leave hairs behind (McDaniel et al. 2000), which can be analyzed for species identification using DNA markers (Mills et al. 2000*a*). At each sampling site, 125 rub-pads were placed in a systematic grid: 25 transects, 3.2 km apart, with each transect consisting of 5 rub-pads, 100 m apart. Pads were checked after 2 weeks. The survey was conducted for 3 years, with an additional pilot year.

Before the survey was initiated, the principal investigators at the University of Montana and at the Rocky Mountain Research Station, U.S. Forest Service, developed reliable DNA-based tests to distinguish lynx from other species based on the degraded and low-quantity samples obtained from single hairs (Mills et al. 2000*a*). Importantly for identification of species of political concern, exhaustive tests to validate the species-identification protocol were conducted prior to initiating the survey (Mills et al. 2000*a,* Mills 2002). These validation tests were included in a detailed protocol sent to all field workers, which also included comprehensive written instructions for all aspects of gathering, labeling, and submitting samples.

After 3 years of sampling, the survey can be considered a success (McKelvey et al. 2002). More than 21,000 pads were placed, and approximately 4,000 samples were processed. About 80% of the hair samples (including single hairs or fragments of hairs) were identified to species. Many other species were detected even though the sampling method was designed to target lynx.

Despite its success in verifying and establishing lynx presence on a nationwide scale, the implementation of the National Lynx Survey identified a challenge broadly relevant to sampling small populations at large scales: the need for field personnel to maintain integrity of all data collected. Despite the detailed written protocol sent to all field-data collectors, a handful of field personnel ignored the protocol and labeled hair from petting zoos and wall mounts as if they were field-collected samples; by sending in these mislabeled samples without informing the principal investigators, they threatened the integrity of the data stream in the nationwide study. A nationwide political and media furor erupted (Mills 2002, Thomas and Pletscher 2002). Fortunately, firewalls were in place in terms of field and lab protocols to protect the scientific integrity of the study to contribute to land management decision-making. Not only were the analyses of the noninvasively collected hair samples fully validated, but also the study design ensured that hair collection in the survey was only the first step in evaluating lynx presence. Follow-up snowtracking and trapping efforts were built into the study to separate actual lynx populations from transient individuals, fur-farm escapees, or mislabeled samples (McKelvey et al. 2002).

Noninvasive DNA sampling opens up the potential for large-scale sampling of distribution and abundance of wide-ranging and small populations. However, the integrity of the samples collected must remain paramount.

not without pitfalls) for both identifying distribution and monitoring abundance of hard-to-sample and rare populations (Mills et al. 2000*a, b;* Oyler-McCance and Leberg 2005).

Even when monitoring abundance in an area where a small population is known to exist, low densities can lead to a low capture or detection probability, which increases sample variance and decreases the likelihood of detecting real declines. The **problem of low power** in monitoring is relevant to all wildlife biology studies (Steidl et al. 1997, Gibbs 2000). It takes on amplified importance in small populations, where failure to detect a decline (Type II error) can lead to extinction (Taylor and Gerrodette 1993, Reed and Blaustein 1997). The concern over inherently low power to reject the null hypothesis of "no decline" for small populations has led to consideration of how to reverse the "burden of proof" for detecting a decline in abundance (Mapstone 1995).

The problem of **high sampling variance** inherent for estimates of abundance in small populations leads to other risks where management plans are based on abundance estimates (e.g., setting recovery goals, harvest levels, or listing under the ESA). An approach to avoiding this problem has been implemented by the National Marine Fisheries Service. In guidelines developed under the Marine Mammal Protection Act, stock assessments are based, in part, on an estimate of minimum population size (U.S. Department of Commerce 1995). The estimated **minimum population size** (N_{min}) is defined as the lower 60% confidence limit of a distribution resulting from a point estimate of abundance and its coefficient of variation. This method increases the probability that population size is equal to or greater than the estimate, accounting for the uncertainty of sampled small populations (Taylor et al. 2000).

The challenges of monitoring trends in abundance, especially for small populations, have led to the development of alternative monitoring frameworks that sidestep abundance and instead rely on **presence–absence, or occupancy** (MacKenzie et al. 2006). In effect, these methods target detection of changes in occupancy measured as the proportion of sampling units where the species is present, correcting for detectability. Although less information is collected at each site than in traditional abundance-based trend monitoring, more sites can be sampled for presence–absence. Indeed, the trade-off of larger scale sampling makes occupancy monitoring an optimal strategy in many cases, especially with cryptic or low-density species and limited funding (Joseph et al. 2006). For example, Witczuk et al. (2008) found that presence–absence sampling was the preferred method for monitoring trends over time of endemic Olympic marmots (*Marmota olympus*) in Olympic National Park.

Finally, we underscore that managers should not deal with the frustrations of monitoring small populations by taking shortcuts in design or study implementation. In particular, **indirect indices of abundance** (e.g., tracks, burrow counts, animal counts uncorrected for detectability) should be implemented only reluctantly and with great care.

Conservation-Reliant Species

In many cases, implementation of well-designed management actions will stabilize or increase the size of a small population to the point that it is expected to persist without further intervention. These successes, whereby population objectives are maintained, are consistent with **societal goals** (e.g., recovery, recreationally viable, ecologically functional). For other species, it is increasingly clear that continued, sometimes intensive management will be required to sustain viable populations. When a species' decline is caused by factors that can be controlled, but not eliminated, it is considered **conservation-reliant** (Scott et al. 2005) and will need continuous intervention to keep risk factors at bay. Conservation reliance is often found when declines are due to ultimate factors that are so widespread or slow to remedy (e.g., habitat loss, competition from invasive species) that treatment of proximate factors such as recruitment or dispersal will be necessary until the ultimate causes of decline can be corrected.

Scott et al. (2005) identified varying degrees of conservation reliance, from species that are entirely dependent on human intervention to those that are able to maintain viable populations once primary threats have been removed. For example, while both the **Aleutian cackling goose** (*Branta hutchinsii leucopareia*, formerly known as the Aleutian Canada goose *B. canadensis leucopareia*) and the Hawaiian stilt were **threatened by nonnative predators** and responded well to **predator removal programs,** their needs for ongoing predator control differ. Aleutian cackling geese nested on small islands and declined due to predation by introduced Arctic foxes (*Vulpes lagopus*). The size of the islands, size of the predator, and **intensive predator-control effort** made it possible to eliminate foxes from the goose's breeding islands, and population size increased to a point that far exceeded recovery goals; **the species was** delisted with no further predator control actions required. **Hawaiian stilts** also declined to small population sizes due to **nonnative predators** (e.g., black rats [*Rattus rattus*], feral cats [*Felis catus*], Indian mongoose [*Herpestes javanicus*]), and **extensive predator-removal efforts** within protected areas have been effective in increasing survival and reproduction of stilts. Because the stilt's predators are found throughout the island of Oahu, however, it has not been possible to eliminate them, and predator control **actions will be required for the foreseeable future** even if numbers of individuals and populations consistent with recovery goals are exceeded.

In reality, most small populations may well require **ongoing conservation actions** to maintain viability even after populations have increased (Scott et al. 2005). Managers will need to identify the conservation measures that not only will most aid recovery, but also must be continued indefinitely to prevent future declines. Here, PVA and sensitivity analysis, in particular, can help. **Sensitivity analysis** can be used to pinpoint management actions that are most likely to contribute to population persistence and compare estimated levels of success for each action, and can help evaluate the need for continuous management. For conservation-reliant species, the population's potential for long-term recovery will rely on the certainty that ongoing management intervention will continue (Scott et al. 2005).

SPECIAL CONSIDERATIONS FOR MANAGING ENDANGERED SPECIES

Permit Requirements for Endangered Species Programs

When a species is listed as endangered or threatened in the United States, **permits are required** to undertake all types of "hands-on" management or any activity, including research, which may disturb the species. Permits can be granted for scientific research or management activities that enhance the welfare of the species.

Applications for permits to manipulate a listed species must be submitted to the U.S. Fish and Wildlife Service or the National Marine Fisheries Service. Once a permit application has been received and accepted as providing the necessary information, a notice is published in the *Federal Register* to allow for public review and comment on the application. Once the review is completed, a permit is issued if the activity is not likely to jeopardize the continued existence of the species.

Scientific permits generally are issued for research and management that will benefit the recovery effort for the species, or for research related to the assessment of threats to the species. In general, permits are not likely to be granted for research that can be accomplished on closely related or surrogate species.

Public Scrutiny of Endangered Species Management

All wildlife management activities are **subject to public review.** However, endangered species conservation and management programs can be especially contentious. Endangered species managers must be prepared for the biological, social, economic, and political controversies that seem inevitably to surround most activities (e.g., Liverman 1990, Clark et al. 1994; see Box 35.4).

Although the **recovery process** prescribed by the Endangered Species Act specifically **avoids issues that are not biologically based,** endangered species managers frequently are asked to defend their biological proposals in arenas where the challenges are nonbiological (Tilt 1989). Designations of **critical habitat** and the attendant need to protect or restore specific areas for the benefit of endangered species often have social and economic effects that precipitate acrimonious debates (e.g., conflicts between northern spotted owl [*Strix occidentalis caurina*] recovery programs and the logging industry in the Pacific Northwest; Doak 1989, Thomas et al. 1990).

Climate Change

The 3 ways (Running and Mills 2009) in which all wildlife populations will **respond to climate change is to move** (e.g., shift geographic range), **adapt** (deal with stressors through plasticity or natural selection), **and/or decline** (e.g., unsuccessful adaptation or movement). To the extent that small wildlife populations exhibit traits such as limited dispersal, high habitat and behavioral specificity, short generation times, and low genetic variability, they will be more prone to decline in the face of novel climate-induced stress; by contrast, the species most likely to prosper through moving and adapting are large populations of generalist invasive and subsidized species (Running and Mills 2009). The ultimate cause of species' declines attributed to climate change is largely out of managers' hands; therefore, it will be critical to enhance a population's capacity to move and adapt. **Potential management actions** include those discussed in this chapter, such as monitoring and improvement of birth and death rates, perhaps with increased importance of population augmentation to offset the effects of limited dispersal and genetic diversity (see also Mills 2007, Scott et al. 2008, Griffin et al. 2009).

SUMMARY

This chapter addresses a range of considerations and tools for managing small populations. It should be clear there is no cookbook approach. The recovery of small populations will be most effective when field data and quantitative tools such as population viability analysis are explicitly incorporated into adaptive management strategies. Because of uncertainties that can affect the persistence and recovery of a small population, managers must be prepared for unexpected problems and adjust their management plans accordingly. Each species and situation presents a unique set of challenges for the manager; the same species may present different management issues in different time periods and different ecological settings. Thus, a modeling framework can be exceptionally helpful to choose among potential management scenarios, and to account for uncertainty in what is known about the species, and what the management will accomplish. Population Viability Analysis is a well-grounded framework for considering dynamics of small and declining wildlife populations. We know that vital rates (e.g., reproduction and survival) are not "created equal" in their effect on population growth or persistence, and that different management alternatives are not equal in the extent that population characteristics can be changed. Thus, sensitivity analyses in the broad sense are a vital component to decide which specific management actions are most likely to aid a small or declining population. As a precautionary and general rule, however, management of small populations should begin early rather than late because, with diminishing population size, a population's vulnerability to extinction increases as management options become more and more constrained.