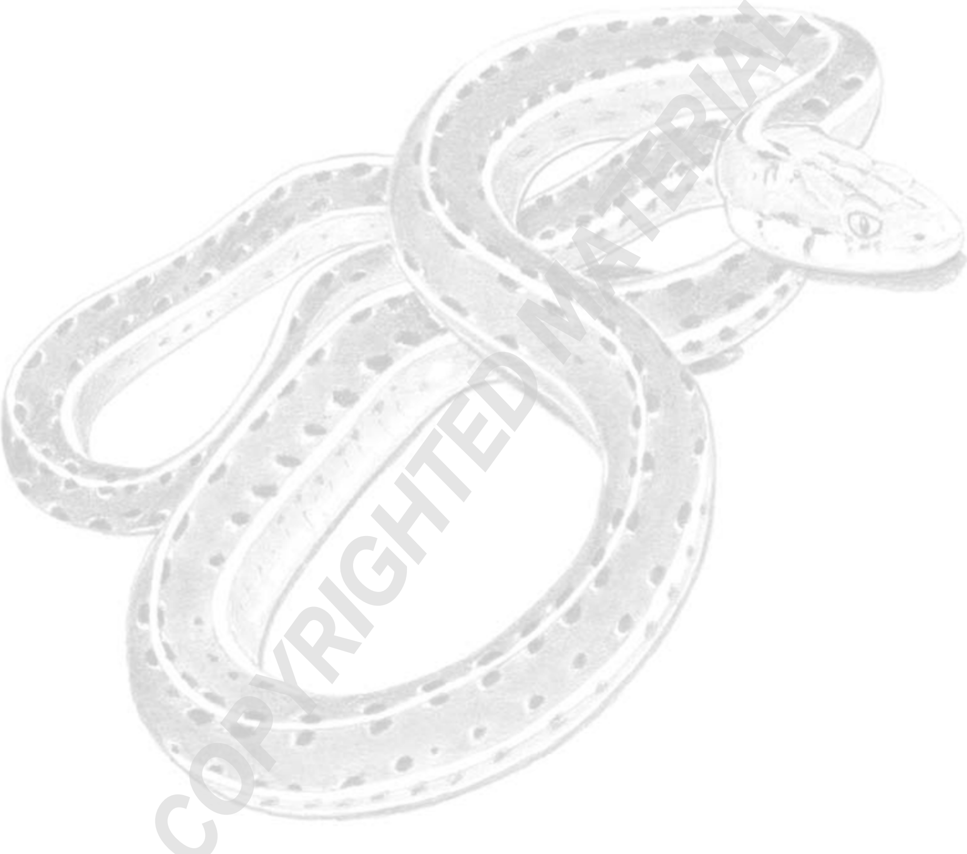
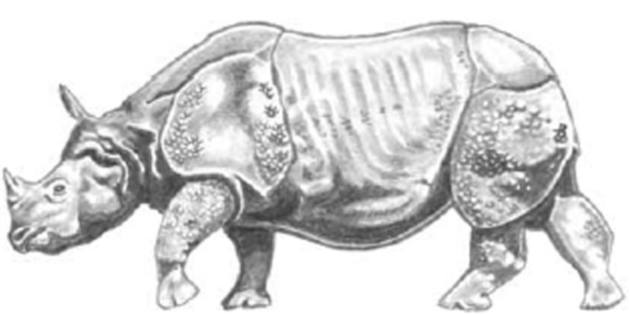
PART I

INTRODUCTION



CHAPTER 1

Introduction



One-horned rhinoceros, Section 5.3

> *We are at a critical juncture for the conservation and study of biological diversity: such an opportunity will never occur again. Understanding and maintaining that diversity is the key to humanity's continued prosperous and stable existence on Earth.*
>
> **US National Science Board Committee on Global Biodiversity (1989)**

> *The extinction of species, each one a pilgrim of four billion years of evolution, is an irreversible loss. The ending of the lines of so many creatures with whom we have traveled this far is an occasion of profound sorrow and grief. Death can be accepted and to some degree transformed. But the loss of lineages and all their future young is not something to accept. It must be rigorously and intelligently resisted.*
>
> **Gary Snyder (1990)**

Chapter Contents

Conservation and the Genetics of Populations, Second Edition. Fred W. Allendorf, Gordon Luikart, and Sally N. Aitken.

We are living in a time of unprecedented extinctions (Myers and Knoll 2001, Stuart *et al.* 2010, Barnosky *et al.* 2011). Current extinction rates have been estimated to be 50–500 times background rates and are increasing; an estimated 3000–30,000 species go extinct annually (Woodruff 2001). Projected extinction rates vary from 5–25% of the world's species by 2015 or 2020. Approximately 23% of mammals, 12% of birds, 42% of turtles and tortoises, 32% of amphibians, 34% of fish, and 9–34% of major plant taxa are threatened with extinction over the next few decades (IUCN 2001, Baillie *et al.* 2004). Over 50% of animal species are considered to be critically endangered, endangered, or vulnerable to extinction (Baillie *et al.* 2004). A recent assessment of the status of the world's vertebrates, based on the International Union for the Conservation of Nature (IUCN) Red List, concluded that approximately 20% are classified as Threatened. This figure is increasing primarily because of agricultural expansion, logging, overexploitation, and invasive introduced species (Hoffmann *et al.* 2010).

The true picture is much worse than this because the conservation status of most of the world's species remains poorly known. Recent estimates indicate that less than 30% of the world's arthropod species have been described (Hamilton *et al.* 2010). Less than 5% of the world's described animal species have been evaluated for the IUCN Red List. Few invertebrate groups have been evaluated, and the evaluations that have been done have tended to focus on molluscs and crustaceans. Among the insects, only the swallowtail butterflies, dragonflies, and damselflies have received much attention.

Conservation biology poses perhaps the most difficult and important questions ever faced by science (Pimm *et al.* 2001). The problems are difficult because they are so complex and cannot be approached by the reductionist methods that have worked so well in other areas of science. Moreover, solutions to these problems require a major readjustment of our social and political systems. There are no more important scientific challenges because these problems threaten the continued existence of our species and the future of the biosphere itself.

1.1 GENETICS AND CIVILIZATION

Genetics has a long history of application to human concerns. The domestication of animals and cultivation of plants is thought to have been perhaps the key step in the development of civilization (Diamond 1997). Early peoples directed genetic change in domestic and agricultural species to suit their needs. It has been estimated that the dog was domesticated over 15,000 years ago, followed by goats and sheep around 10,000 years ago (Darlington 1969, Zeder and Hess 2000). Wheat and barley were the first crops to be domesticated in the Old World approximately 10,000 years ago; beans, squash, and maize were domesticated in the New World at about the same time (Darlington 1969, Kingsbury 2009).

The initial genetic changes brought about by cultivation and domestication were not due to intentional selection but apparently were inadvertent and inherent in cultivation itself. Genetic change under domestication was later accelerated by thousands of years of purposeful selection as animals and crops were selected to be more productive or to be used for new purposes. This process became formalized in the discipline of agricultural genetics after the rediscovery of Mendel's principles at the beginning of the 20th century.

The 'success' of these efforts can be seen everywhere. Humans have transformed much of the landscape of our planet into croplands and pasture to support the over 7 billion humans alive today. It has been estimated that 35% of the Earth's ice-free land surface is now occupied by crops and pasture (Foley *et al.* 2007), and that 24% of the primary terrestrial productivity is used by humans (Haberl *et al.* 2007). Recently, however, we have begun to understand the cost at which this success has been achieved. The replacement of wilderness by human-exploited environments is causing the rapidly accelerating loss of species and ecosystems throughout the world. The continued growth of the human population and their direct and indirect effects on environments imperils a large proportion of the wild species that now remain.

Aldo Leopold inspired a generation of biologists to recognize that the actions of humans are embedded into an ecological network that should not be ignored (Meine 1998). The organized actions of humans are controlled by sociopolitical systems that operate into the future on a timescale of a few years at most. All too often our systems of conservation are based on the economic interests of humans in the immediate future. We tend to disregard, and often mistreat, elements that lack economic value but that are essential to the stability of the ecosystems upon which our lives and the future of our children depend.

In 1974, Otto Frankel published a landmark paper entitled 'Genetic conservation: our evolutionary responsibility', which set out conservation priorities:

> *First, . . . we should get to know much more about the structure and dynamics of natural populations and communities. . . . Second, even now the geneticist can play a part in injecting genetic considerations into the planning of reserves of any kind. . . . Finally, reinforcing the grounds for nature conservation with an evolutionary perspective may help to give conservation a permanence which a utilitarian, and even an ecological grounding, fail to provide in men's minds.*

Frankel, an agricultural plant geneticist, came to the same conclusions as Leopold, a wildlife biologist, by a very different path. In Frankel's view, we cannot anticipate the future world in which humans will live in a century or two. Therefore, it is our responsibility to "keep evolutionary options open". It is time to apply our understanding of genetics to conserving the natural ecosystems that are threatened by human civilization.

1.2 WHAT SHOULD WE CONSERVE?

Conservation can be viewed as an attempt to protect the genetic diversity that has been produced by evolution over the previous 3.5 billion years on our planet (Eisner *et al.* 1995). Genetic diversity is one of three forms of biodiversity recognized by the IUCN as deserving conservation, along with species and ecosystem diversity (www.cbd.int, McNeely *et al.* 1990). Unfortunately, genetics has been generally ignored by the member countries in their National Biodiversity Strategy and Action Plans developed to implement the Convention on Biological Diversity (CBD) (Laikre *et al.* 2010a).

We can consider the implications of the relationship between genetic diversity and conservation at many levels: genes, individuals, populations, varieties, subspecies, species, genera, and so on. Genetic diversity provides a retrospective view of evolutionary lineages of taxa (phylogenetics), a snapshot of the current genetic structure within and among populations (population and ecological genetics), and a glimpse ahead to the future evolutionary potential of populations and species (evolutionary biology).

1.2.1 Phylogenetic diversity

The amount of genetic divergence based upon **phylogenetic** relationships is often considered when setting conservation priorities for different species (Mace *et al.* 2003, Avise 2008). For example, the United States Fish and Wildlife Service (USFWS) assigns priority for listing under the Endangered Species Act (ESA) of the United States on the basis of "taxonomic distinctiveness" (USFWS 1983). Species of a **monotypic** genus receive the highest priority. The tuatara raises several important issues about assigning conservation value and allocating our conservation efforts based upon taxonomic distinctiveness (Example 1.1).

Faith (2008) recommends integrating evolutionary processes into conservation decision-making by considering phylogenetic diversity. Faith provides an approach that goes beyond earlier recommendations that species that are taxonomically distinct deserve greater conservation priority. He argues that the phylogenetic diversity approach provides two ways to consider maximizing biodiversity. First, considering phylogeny as a product of evolutionary process enables the interpretation of diversity patterns to maximize biodiversity for future evolutionary change. Second, phylogenetic diversity also provides a way to better infer biodiversity patterns for poorly described taxa when used in conjunction with information about geographic distribution.

Vane-Wright *et al.* (1991) presented a method for assigning conservation value on the basis of phylogenetic relationships. This system is based upon the information content of the topology of a particular phylogenetic hierarchy. Each extant species is assigned an index of taxonomic distinctness that is inversely proportional to the number branching points to other extant lineages. May (1990) has estimated that the tuatara (Example 1.1) represents between 0.3 and 7% of the taxonomic distinctness, or perhaps we could say genetic information, among reptiles. This is equivalent to saying that each of the two tuatara species is equivalent to approximately 10 to 200 of the 'average' reptile species. Crozier and Kusmierski (1994) developed an approach to setting conservation priorities based upon phylogenetic relationships and genetic divergence among taxa. Faith (2002) has presented a method for quantifying biodiversity for the purpose of identifying conservation priorities that considers phylogenetic diversity both between and within species.

Example 1.1 The tuatara: a living fossil

The tuatara is a lizard-like reptile that is the remnant of a taxonomic group that flourished over 200 million years ago during the Triassic Period (Figure 1.1). Tuatara are now confined to some 30 small islands off the coast of New Zealand (Daugherty *et al*. 1990). Three species of tuatara were recognized in the 19th century. One of these species is now extinct. A second species, *Sphenodon guntheri*, was ignored by legislation designed to protect the tuatara which 'lumped' all extant tuatara into a single species, *S. punctatus*.

Daugherty *et al*. (1990) reported allozyme and morphological differences from 24 of the 30 islands on which tuatara are thought to remain. These studies support the status of *S. guntheri* as a distinct species and indicate that fewer than 300 individuals of this species remain on a single island, North Brother Island in Cook Strait. Another population of *S. guntheri* became extinct earlier in this century. Daugherty *et al*. (1990) argued that not all tuatara populations are of equal conservation value. As the last remaining population of a distinct species, the tuatara on North Brother Island represent a greater proportion of the genetic diversity remaining in the genus *Sphenodon* and deserve special recognition and protection. However, recent results with other molecular techniques indicate that the tuatara on North Brother Island probably do not warrant recognition as a distinct species (Hay *et al*. 2010, Example 16.3).

Figure 1.1 Adult male tuatara.

On a larger taxonomic scale, how should we value the tuatara relative to other species of reptiles? Tuatara species are the last remaining representatives of the Sphenodontida, one of four extant orders of reptiles (tuatara, snakes and lizards, alligators and crocodiles, and tortoises and turtles). In contrast, there are approximately 5000 species in the Squamata, the speciose order that contains lizards and snakes.

One position is that conservation priorities should regard all species as equally valuable. This position would equate the two tuatara species with any two species of reptiles. Another position is that we should take phylogenetic diversity into account in assigning conservation priorities. The extreme phylogenetic position is that we should assign equal conservation value to each major sister group in a phylogeny. According to this position, tuatara would be weighed equally with the over 5000 species of other snakes and lizards. Some intermediate between these two positions seems most reasonable.

There is great appeal to placing conservation emphasis on distinct evolutionary lineages with few living relatives. Living fossils, such as the tuatara, ginkgo (Royer *et al*. 2003), or the coelacanth (Thompson 1991), represent important pieces in the jigsaw puzzle of evolution. Such species are relics that are representatives of taxonomic groups that once flourished. Study of the primitive morphology, physiology, and behavior of living fossils can be extremely important in understanding evolution. For example, tuatara morphology has hardly changed in nearly 150 million years. Among the many primitive features of the tuatara is a rudimentary third, or pineal, eye on the top of the head.

Tuatara represent an important ancestral outgroup for understanding vertebrate evolution. For example, a recent study has used genomic information from tuatara to reconstruct and understand the evolution of 18 human retroposon elements (Lowe *et al*. 2010). Most of these elements were quickly inactivated early in the mammalian lineage, and thus study of other mammals provides little insight into these elements in humans. These authors conclude that species with historically low population sizes (such as tuatara) are more likely to maintain ancient mobile elements for long periods of time with little change. Thus, these species are indispensable in understanding the evolutionary origin of functional elements in the human genome.

In contrast, others have argued that our conservation strategies and priorities should be based primarily upon conserving the evolutionary process rather than preserving only those pieces of the evolutionary puzzle that are of interest to humans (Erwin 1991). Those species that will be valued most highly under the schemes that weigh phylogenetic distinctness are those that may be considered evolutionary failures. Evolution occurs by changes within a single evolutionary lineage (**anagenesis**) and the branching of a single evolutionary lineage into multiple lineages (**cladogenesis**). Conservation of primitive, nonradiating taxa is not likely to be beneficial to the protection of the evolutionary process and the environmental systems that are likely to generate future evolutionary diversity (Erwin 1991).

Figure 1.2 illustrates the phylogenetic relations among seven hypothetical species (from Erwin 1991). Species A and B are phylogenetically distinct taxa that are endemic to small geographic areas (e.g., tuataras in New Zealand). Such lineages carry information about past evolutionary events, but they are relatively unlikely to be sources of future evolution. In contrast, the stem resulting in species C, D, E, and F is relatively likely to be a source of future anagenesis and cladogenesis. In addition, species such as C, D, E, and F may be widespread, and therefore are not likely to be the object of conservation efforts.

The problem is more complex than just identifying species with high conservation value; we must take a broader view and consider the habitats and environments where our conservation efforts could be concentrated. Conservation emphasis on phylogenetically distinct species will lead to protection of environments that are not likely to contribute to future evolution (e.g., small islands along the coast of New Zealand). In contrast, geographic areas that are the center of evolutionary activity for diverse taxonomic groups could be identified and targeted for long-term protection.

Recovery from our current extinction crisis should be a central concern of conservation (Myers *et al.* 2000). It is important to maintain the potential for the generation of future biodiversity. We should identify and protect contemporary hotspots of evolutionary radiation and the functional taxonomic group from which tomorrow's biodiversity is likely to originate. In addition, we should protect those phylogenetically distinct species that are of special value for our understanding of biological diversity and the evolutionary process. These species are also potentially valuable for future evolution of biodiversity because of their combination of unusual phenotypic characteristics that may give rise to a future evolutionary radiation. Isaac *et al.* (2007) have proposed using an index that combines both evolutionary distinctiveness and IUCN Red List categories to set conservation priorities.

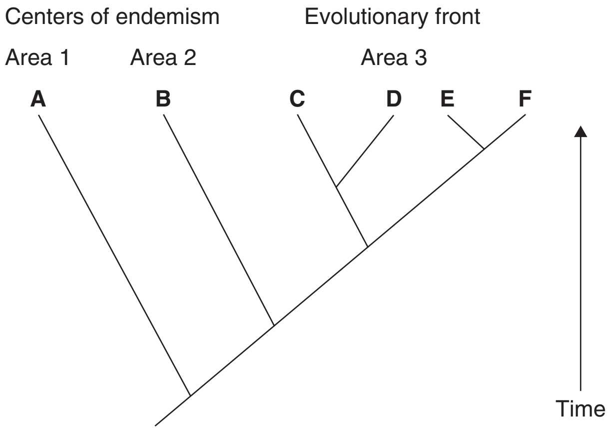


Figure 1.2 Hypothetical phylogeny of seven species. Redrawn from Erwin (1991).

1.2.2 Populations, species, or ecosystems?

A related, and sometimes impassioned, dichotomy between protecting centers of biodiversity or phylogenetically distinct species is the dichotomy between emphasis on species conservation or on the conservation of habitat or ecosystems (Soulé and Mills 1992, Armsworth *et al.* 2007). Conservation efforts to date have emphasized the concerns of individual species. For example, in the US the Endangered Species Act (ESA) has been the legal engine behind much of the conservation efforts. However, it is frustrating to see enormous resources being spent on a few high profile species when little is spent on less charismatic taxa or in preventing environmental deterioration that would benefit many species. It is clear that a more comprehensive and proactive conservation strategy emphasizing protection of habitat and ecosystems, rather than species, is needed. Some have advocated a shift from saving things, the products of evolution (species, communities, or ecosystems), to saving the underlying processes of evolution "that underlie a dynamic biodiversity at all levels" (Templeton *et al.* 2001).

It has been argued that more concern about extinction should be focused on the extinction of genetically distinct populations, and less on the extinction of species (Hughes *et al.* 1997, Hobbs and Mooney 1998). The conservation of many distinct populations is required to maximize evolutionary potential of a species and to minimize the long-term extinction risks of a species. In addition, a population focus would also help to prevent costly and desperate 'last-minute' conservation programs that occur when only one or two small populations of a species remain. The first attempt to estimate the rate of population extinction worldwide was published by Hughes *et al.* (1997). They estimated that tens of millions of local populations that are genetically distinct go extinct each year. Approximately 16 million of the world's three billion genetically distinct natural populations go extinct each year in tropical forests alone.

Luck *et al.* (2003) have considered the effect of population diversity on the functioning of ecosystems and so-called **ecosystem services**. They argue that the relationship between biodiversity and human wellbeing is primarily a function of the diversity of populations within species. They have also proposed a new approach for describing population diversity that considers the value of groups of individuals to the services that they provide.

Ceballos and Ehrlich (2002) have compared the historical and current distributions of 173 declining mammal species from throughout the world. Their data included all of the terrestrial mammals of Australia and subsets of terrestrial mammals from other continents. Nearly 75% of all species they included have lost over 50% of their total geographic range. Approximately 22% of all Australian species are declining, and they estimated that over 10% of all Australian terrestrial mammal populations have been extirpated since the 19th century. These estimates, however, all assume that population extirpation is proportional to loss of range area rather than defining populations using genetic criteria.

The amount of genetic variation within a population may also play an important ecosystem role in the relationships among species in some functional groups and ecosystems. Clark (2010) has found that intraspecific genetic variation within forest trees in the southeastern US allows higher species diversity. Recent results in **community genetics** suggest that individual alleles within some species can affect community diversity and composition (Crutsinger *et al.* 2006). For example, alleles at tannin loci in cottonwood trees affect palatability and decay rate of leaves, which in turn influences abundance of soil microbes, fungi, and arboreal insects and birds (Whitham *et al.* 2008). Genetic variation in the bark characteristics of a **foundation species** (Tasmanian blue gum tree) has been found to affect the abundance and distribution of insects, birds, and marsupials. Loss or restoration of such alleles to populations could thus influence community diversity and ecosystem function (Whitham *et al.* 2008).

Conservation requires a balanced approach that is based upon habitat protection which also takes into account the natural history and viability of individual species. Consider Chinook salmon in the Snake River basin of Idaho, which are listed under the ESA. These fish spend their first two years of life in small mountain rivers and streams far from the ocean. They then migrate over 1500 km downstream through the Snake and Columbia Rivers and enter the Pacific Ocean. There they spend two or more years ranging as far north as the coast of Alaska before they return to spawn in their natal freshwater streams. There is no single ecosystem that encompasses these fish, other than the biosphere itself. Protection of this species requires a combination of habitat measures and management actions that take into account the complex life-history of these fish.

1.3 HOW SHOULD WE CONSERVE BIODIVERSITY?

Extinction is a **demographic** process: the failure of one generation to replace itself with a subsequent generation. Demography is of primary importance in managing populations for conservation (Lacy 1988, Lande 1988). Populations are subject to uncontrollable **stochastic** demographic factors as they become smaller. It is possible to estimate the expected mean and variance of a population's time to extinction if one has an understanding of a population's demography and environment (Goodman 1987, Belovsky 1987, Lande 1988).

There are two main types of threats causing extinction: **deterministic** and **stochastic** threats (Caughley 1994). Deterministic threats are habitat destruction, pollution, overexploitation, species translocation, and global climate change. Stochastic threats are random changes in genetic, demographic or environmental factors. Genetic stochasticity is random genetic change (drift) and increased inbreeding (Shaffer 1981). Genetic stochasticity leads to loss of genetic variation (including beneficial alleles) and increase in frequency of harmful alleles. An example of demographic stochasticity is random variation in sex ratios, for example producing only male offspring. Environmental stochasticity is simply random environmental variation, such as the occasional occurrence of several harsh winters in a row. In a sense, the effects of small population size are both deterministic and stochastic. We know that genetic drift in small populations is likely to have harmful effects, and the smaller the population, the greater the probability of such effects. However, the effects of small population size are stochastic because we cannot predict what traits will be affected.

Under some conditions, extinction is likely to be influenced by genetic factors. Small populations are also subject to genetic stochasticity, which can lead to loss of genetic variation through genetic drift. The 'inbreeding effect of small populations' (see Box 1.1) is likely to lead to a reduction in the fecundity and viability of individuals in small populations. For example, Frankel and Soulé (1981, p. 68) suggested that a 10% decrease in genetic variation due to the inbreeding effect of small populations is likely to cause a 10–25% reduction in reproductive performance of a population. This in turn is likely to cause a further reduction in population size, and thereby reduce a population's ability to persist (Gilpin and Soulé 1986). This has come to be known as the **extinction vortex** (see Figure 14.2).

Some have argued that genetic concerns can be ignored when projecting the viability of small populations because they are in much greater danger of extinction by purely demographic stochastic effects (Lande 1988, Pimm *et al.* 1988, Caughley 1994, Frankham 2003, Sarre and Georges 2009). It has been argued that such small populations are not likely to persist long enough to be affected by inbreeding depression, and that efforts to reduce demographic stochasticity will also reduce the loss of genetic variation. The disagreement over whether or not genetics should be considered in demographic predictions of population persistence has been unfortunate and

Box 1.1 What is an 'inbred' population?

The term 'inbred population' is used in the literature to mean two very different things (Chapter 13, Templeton and Read 1994). In the conservation literature, 'inbred population' is often used to refer to a small population in which mating between related individuals occurs because after a few generations, all individuals in a small population will be related. Thus, matings between related individuals (inbreeding) will occur in small populations even if they are random mating (panmictic). This has been called the 'inbreeding effect of small populations' (see Chapter 6).

Formally in population genetics, an 'inbred' population is one in which there is a tendency for related individuals to mate with one another. For example, many extremely large populations of pine trees are inbred because of their spatial structure (see Section 9.2). Nearby trees tend to be related to one another because of limited seed dispersal, and nearby trees also tend to fertilize each other because of wind pollination. Therefore, a population of pine trees with millions of individuals may still be 'inbred'.

Population genetics is a complex field. The incorrect, ambiguous, or careless use of words can sometimes result in unnecessary confusion. We have made an effort throughout this book to use words precisely and carefully.

misleading. Extinction is a demographic process that is likely to be influenced by genetic effects under some circumstances. The important issue is to determine under what conditions genetic concerns are likely to influence population persistence (Nunney and Campbell 1993).

Perhaps most importantly, we need to recognize when management recommendations based upon demographic and genetic considerations may be in conflict with each other. For example, small populations face a variety of genetic and demographic effects that threaten their existence. Management plans aim to increase the population size as soon as possible to avoid the problems associated with small populations. However, efforts to maximize growth rate may actually increase the rate of loss of genetic variation by relying on the exceptional reproductive success of a few individuals (see Example 19.1, Caughley 1994).

Ryman and Laikre (1991) considered what they termed **supportive breeding** in which a portion of wild parents are brought into captivity for reproduction and their offspring are released back into the natural habitat where they mix with wild conspecifics. Programs similar to this are carried out in a number of species to increase population size and thereby temper stochastic demographic effects (e.g., Blanchet *et al.* 2008). Under some circumstances, supportive breeding may reduce effective population size and cause a drastic reduction in genetic heterozygosity (Ryman 1994).

Genetic information also can provide valuable insight into the demographic structure and history of a population (Escudero *et al.* 2003). Estimation of the number of unique genotypes can be used to estimate total population size in populations that are difficult to census (Luikart *et al.* 2010). Many demographic models assume a single random mating population. Examination of the distribution of genetic variation over the distribution of a species can identify what geographic units can be considered separate demographic units. Consider the simple example of a population of trout found within a single small lake for which it would seem appropriate to consider these fish a single demographic unit. However, under some circumstances the trout in a single small lake can actually represent two or more separate reproductive (and demographic) groups with little or no exchange between them (e.g., Ryman *et al.* 1979).

The issue of population persistence is a multidisciplinary problem that involves many aspects of the biology of the populations involved (Lacy 2000b). A similar statement can be made about most of the issues we are faced with in conservation biology. We can only resolve these problems by an integrated approach that incorporates demography and genetics, as well as other biological considerations that are likely to be critical for a particular problem (e.g., behavior, physiology, interspecific interactions, as well as habitat loss and environmental change).

1.4 APPLICATIONS OF GENETICS TO CONSERVATION

Darwin (1896) was the first to consider the importance of genetics in the persistence of natural populations. He expressed concern that deer in British nature parks may be subject to loss of vigor because of their small population size and isolation. Voipio (1950) presented the first comprehensive consideration of the application of population genetics to the management of natural populations. He was primarily concerned with the effects of genetic drift in game populations that were reduced in size by trapping or hunting and fragmented by habitat loss.

The modern concern for genetics in conservation began around 1970 when Sir Otto Frankel (Frankel 1970) began to raise the alarm about the loss of primitive crop varieties and their replacement by genetically uniform cultivars (see Guest Box 1). It is not surprising that these initial considerations of conservation genetics dealt with species that were used directly as resources by humans. Conserving the genetic resources of wild relatives of agricultural species remains an important area of conservation genetics (Maxted 2003, Hanotte *et al.* 2010). A surprisingly modern view of the importance and role of genetics in conservation was written by J.C. Greig in 1979. This interesting paper emphasized the importance of maintaining the integrity of local population units.

The application of genetics to conservation in a more general context did not blossom until around 1980, when three books established the foundation for applying the principles of genetics to conservation of biodiversity (Soulé and Wilcox 1980, Frankel and Soulé 1981, Schonewald-Cox *et al.* 1983). Today conservation genetics is a well-established discipline, with its own journals (*Conservation Genetics* and *Conservation Genetics Resources*) and two textbooks, including this one and Frankham *et al.* (2010).

Maintenance of biodiversity primarily depends upon the protection of the environment and maintenance of habitat. Nevertheless, genetics has played an important and diverse role in conservation biology in the last few years. Nearly 10% of the articles published in the journal *Conservation Biology* since its inception in 1988 have "genetic" or "genetics" in their title. Probably at least as many other articles deal with largely genetic concerns but do not have the term in their title. Thus, some 15% of the articles published in *Conservation Biology* have genetics as a major focus.

The subject matter of papers published on conservation genetics is extremely broad. However, most of articles dealing with conservation and genetics fit into one of the five broad categories below:

1. Management and reintroduction of captive populations, and the restoration of biological communities.
2. Description and identification of individuals, genetic population structure, kin relationships, and taxonomic relationships.
3. Detection and prediction of the effects of habitat loss, fragmentation, and isolation.
4. Detection and prediction of the effects of hybridization and introgression.
5. Understanding the relationships between adaptation or fitness and genetic characters of individuals or populations.

These topics are listed in order of increasing complexity and decreasing uniformity of agreement among conservation geneticists. Although the appropriateness of captive breeding in conservation has been controversial (Snyder *et al.* 1996, Adamski and Witkowski 2007, Fraser 2008), procedures for genetic management of captive populations are well developed with relatively little controversy. However, the relationship between specific genetic types and fitness or adaptation has been a particularly vexing issue in evolutionary and conservation genetics. Nevertheless, studies have shown that natural selection can bring about rapid genetic changes in populations that may have important implications for conservation (Stockwell *et al.* 2003).

Invasive species are recognized as one of the top two threats to global biodiversity (Chapter 20). Studies of genetic diversity and the potential for rapid evolution of invasive species may provide useful insights into what causes species to become invasive (Lee and Gelembiuk 2008). More information about the genetics and evolution of invasive species or native species in invaded communities, as well as their interactions, may lead to predictions of the relative susceptibility of ecosystems to invasion, identification of key alien species, and predictions of the subsequent effects of removal.

Recent advances in molecular genetics, including sequencing of the entire genomes of many species, have revolutionized applications of genetics (e.g., medicine, forestry, and agriculture). For example, it has been suggested that genetic engineering should be considered as a conservation genetics technique (Adams *et al.* 2002). Many native trees in the northern temperate zone have been devastated by introduced diseases for which little or no genetic resistance exists (e.g., European and North American elms, and the North American chestnut. Adams *et al.* (2002) suggested that transfer of resistance genes by genetic modification is perhaps the only available method for preventing the loss of important tree species. Transgenic trees have been developed for both American elm and American chestnut, and are now being tested for stable resistance to Dutch elm disease and chestnut blight (Newhouse *et al.* 2007). The use of genetic engineering to improve crop plants has been very controversial. There no doubt will continue to be a lively debate in the near future about the use of these procedures to prevent the extinction of natural populations.

The loss of key tree species is likely to affect many other species as well. For example, whitebark pine is currently one of the two most important food resources for grizzly bears in the Yellowstone National Park ecosystem (Mattson and Merrill 2002). However, virtually all of the whitebark pine in this region is projected to be **extirpated** because of an exotic pathogen (Mattson *et al.* 2001), and with predicted geographic shifts in the climatic niche-based habitat of this species in the next century (Warwell *et al.* 2007).

There are a variety of efforts around the world to store samples of DNA libraries, frozen cells, gametes, and seeds that could yield DNA (Frozen Ark Project, Millennium Seed Bank Project, Svalbard Global Seed Vault, Ryder *et al.* 2000). The hope is that these resources would at least provide complete genome sequences of species that might become extinct in the not-distant future. These sequences could be invaluable for reconstructing evolutionary relationships, understanding how specific genes arose to encode proteins that perform specialized functions, and how the regulation of genes has evolved. In some cases (e.g., seed banks), these resources could be used to recover apparent extinct species.

1.5 THE FUTURE

Genetics is likely to play even a greater role in conservation biology in the future (Primmer 2009, Ouborg *et al.* 2010, Avise 2010, Frankham 2010). We will soon have complete genome sequences from thousands of species, as well as many individuals within species (Haussler *et al.* 2009). This coming explosion of information will transform our understanding of the amount, distribution, and functional significance of genetic variation in natural populations (Amato *et al.* 2009, Allendorf *et al.* 2010). Now is a crucial time to explore the potential implications of this information revolution for conservation genetics, as well as to recognize limitations in applying genomic tools to conservation issues. The ability to examine hundreds or thousands of genetic markers with relative ease will make it possible to answer many important questions in conservation that have been intractable until now (Figure 1.3).

As in other areas of genetics, model organisms have played an important research role in conservation genetics (Frankham 1999). Many important theoretical issues in conservation biology cannot be answered by research on threatened species (e.g., how much gene flow is required to prevent the inbreeding effects of small population size?). Such empirical questions are often best resolved in species that can be raised in captivity in large numbers with a rapid generation interval (e.g., the fruit fly *Drosophila*, the guppy, deer mouse, and the fruit-fly equivalent in plants, *Arabidopsis*). The genome sequencing of plant and animal model and agricultural species have been crucial for transferring genomic tools to wild populations of other

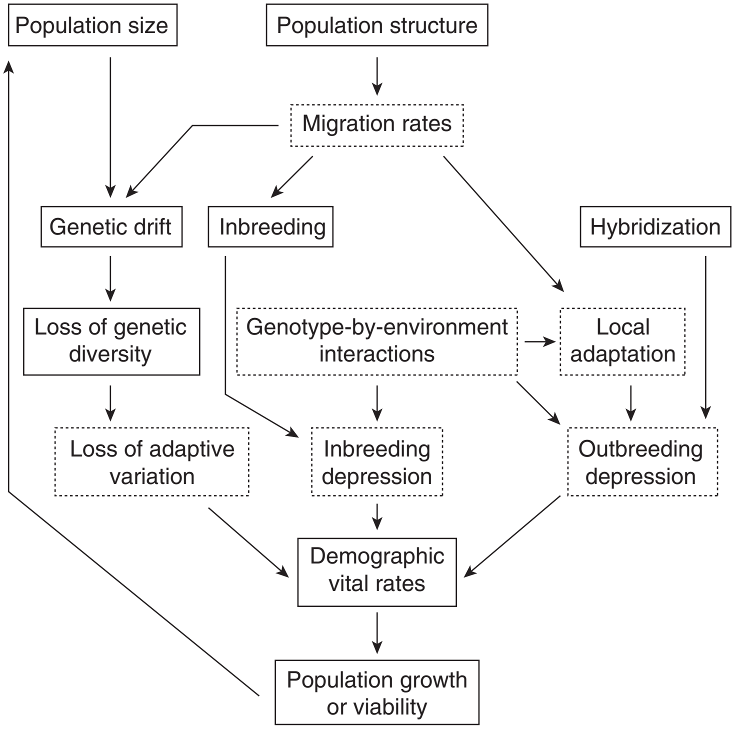


Figure 1.3 Schematic diagram of interacting factors in the conservation of natural populations. Traditional conservation genetics, using neutral markers, provides direct estimates of some of these factors (outlined by solid lines). Conservation genomics can address a wider range of factors (outlined by dashed lines). It also promises more precise estimates of neutral processes and understanding of the specific genetic basis of all of these factors. For instance, traditional conservation genetics can estimate overall migration rates or inbreeding coefficients, while genomic tools can assess gene flow rates specific to adaptive loci or founder-specific inbreeding coefficients. From Allendorf *et al.* (2010).

species. Such laboratory investigations can also provide excellent training opportunities for students. We have tried to provide a balance of examples from model and threatened species. Nevertheless, where possible we have chosen examples from threatened species, even though many of the principles were first demonstrated with model species.

This is an exciting time to be interested in the genetics of natural populations. Molecular techniques make it possible to detect genetic variation in any species of interest, not just those that can be bred and studied in the laboratory (Wayne and Morin 2004, Allendorf *et al*. 2010). However, interpretation of this explosion of data requires a solid understanding of population genetics theory (see Preface, Figure i.1). This book is meant to provide a thorough examination of our understanding of the genetic variation in natural populations. Based upon that foundation, we will consider the application of this understanding to the many problems faced by conservation biologists, with the hope that our more informed actions can make a difference.

Guest Box 1 The role of genetics in conservation

L. Scott Mills and Michael E. Soulé

Until recently, most conservationists ignored genetics and most geneticists ignored the biodiversity catastrophe. It was agricultural geneticists, led by Sir Otto Frankel (1974), who began to sound an alarm about the disappearance of thousands of land races – crop varieties coaxed over thousands of years to adapt to local soils, climates, and pests. Frankel challenged geneticists to help promote an "evolutionary ethic" focused on maintaining evolutionary potential and food security in a rapidly changing world.

Frankel's pioneering thought inspired the first international conference on conservation biology in 1978. It brought together ecologists and evolutionary geneticists to consider how their fields could help slow the extinction crisis. Some of the chapters in the proceedings (Soulé and Wilcox 1980) foreshadowed population viability analysis and the interactions of demography and genetics in small populations (the extinction vortex). Several subsequent books (Frankel and Soulé 1981, Schonewald-Cox *et al*. 1983, Soulé 1987a) consolidated the role of genetic thinking in nature conservation.

Thus, topics such as inbreeding depression and loss of heterozygosity were prominent since the beginning of the modern discipline of conservation biology, but like inbred relatives, they were conveniently forgotten at the end of the 20th century. Why? Fashion. Following the human proclivity to champion simple, singular solutions to complex problems, a series of papers on population viability in the late 1980s and early 1990s argued that – compared with demographic and environmental accidents – inbreeding and loss of genetic variation were trivial contributors to extinction risk in small populations. Eventually, however, this swing in scientific fashion was arrested by the friction of real world complexity.

Thanks to the work of F_1 and F_2 conservation geneticists, it is now clear that inbreeding depression can increase population vulnerability by interacting with random environmental variation, not to mention deterministic factors including habitat degradation, new diseases, and invasive exotics. Like virtually all dualisms, the genetic versus nongenetic battles abated in the face of the overwhelming evidence for the relevance of both.

Genetic approaches have become prominent in other areas of conservation biology as well. These include: (1) the use of genetic markers in forensic investigations concerned with wildlife and endangered species; (2) genetic analyses of hybridization and invasive species; (3) noninvasive genetic estimation of population size and connectivity; and (4) studies of taxonomic affiliation and distance. And, of course, the overwhelming evidence of rapid climate change has renewed interest in the genetic basis for adaptation as presaged by Frankel 30 years ago. Nowadays, genetics is an equal partner with ecology, systematics, physiology, epidemiology, and behavior in conservation, and both conservation and genetics are enriched by this pluralism.