

Chapter 1

The History and Scope of Genetics in Conservation

1.1 Evolution and Conservation

Conservation and evolution are inseparable. Conservation is about ensuring that biological diversity, and the natural processes that sustain it, is protected over short and long time scales. This effort must acknowledge that we are in a time of rapid and extensive change to natural systems wrought by the activities of a single species, *Homo sapiens*. Evolutionary processes determine the response of a species to changes in the biotic and physical environment and, thus, population viability under current and future conditions. It follows that the concepts and tools of evolutionary biology are essential to the challenge of conservation biology in several ways:

- To understand the natural processes that have shaped and sustain biological diversity
- To understand how human-driven changes to the environment alter the direction and rate of evolutionary change, and
- To predict how the products of past evolution will respond to this, to identify management priorities and strategies and methods for monitoring the effectiveness of these.

In a seminal paper, Frankel (1974: 54) defined an evolutionary ethic that should underly efforts to conserve natural populations and systems:

“In this context, genetics has social responsibilities in two directions: first, to collaborate in planning the biological system of conservation so as to establish the highest possible evolutionary potential; second, to help in establishing an evolutionary ethic, as part of our social ethics, which will make it acceptable and indeed inevitable for civilized man to regard the continuing existence of other species as an integral part of his own existence. This demands continuing evolution.”

Continued evolution cannot occur without attention to maintaining the viability of populations and the integrity of natural environments. In this context, Frankel’s sentiments can be reworded as the following general goal for conservation:

To maintain evolutionary processes and the viability of species and functional landscapes necessary to achieve this.

We have written this book to put flesh on this skeletal goal. Specifically, we seek to explore how an understanding of evolutionary principles, together with the tools and concepts of modern genetics, can promote effective conservation. In this introductory chapter, we provide a context for the remainder of the book by reviewing briefly the history of conservation genetics and its current and potential scope and considering the implications of evolutionary thinking for management of threatened systems.

1.2 Historical foundations of Conservation Genetics

Modern Conservation Biology is notable for encompassing a wide variety of disciplines in biology and social sciences, drawing from and combining these as necessary (Soule 1986). The use of genetic theory and methods in conservation has a long history, although the significance accorded to genetic information and processes has varied. Like many areas of conservation biology, application of conservation genetics principles in practical management of natural populations has been limited, partly because of limited resources or information, but also due to perceived low priority relative to other issues.

Conservation Genetics is primarily founded from experience gained in genetic manipulation of plants and animals for agriculture, combined with the sciences of population and quantitative genetics developed from the 1920s (Figure 1.1). Humans have long valued different breeds and varieties of domesticated species and manipulated these for production or aesthetic purposes. Examples abound, for example from domestication and morphological selection among dog breeds (Wayne 1999), domestication of Cassava from wild *Manihot esculenta* populations in the southern Amazon several thousand years ago (Olsen & Schaal 1999), development of hybrid and polyploid cereals in the middle east, and so on. Culminating in the work of Mendel (1866), plant breeders made a central contribution to elucidating the physical basis of inheritance in 19th century and continued to do so through much of the 20th centuries, and continue to do so (eg. McClintock 1978).

From the development of the theory of evolution (Darwin 1859, Wallace 1858) and its reconciliation with mechanisms of inheritance followed the “neoDarwinian synthesis”, a rapid development of population and quantitative genetics (Fisher 1930, Wright 1931, Haldane 1932, Falconer 1960) directed in part at increasing the efficiency of genetic improvement of domesticated species. Another important

corollary of these activities was that the gene became recognized as a fundamental level of biological organization and diversity (see Chapter 8).

Through the following decades, the economic value of genetic variety, or "genetic resources" was identified and the issue of preserving genetic diversity of domesticates came to the fore (Frankel & Soule 1981). This was accorded such importance that international institutions were established to maintain germ plasm from different varieties of agriculturally significant crop species and, to a lesser extent, domesticated animals. The impact of human activities on natural reservoirs of genetic diversity (Brown 1992), including issues arising from newly developed transgenic strains (see Chapter 12), remains a major concern. With the increased appreciation of the potential value of genetic variation in natural populations, have come assertions of sovereign ownership of genetic resources, an issue that was prominent in negotiating the 1992 Convention on Biological Diversity and to which we return in Chapter 8.

From the experience of agricultural genetics and the parallel development of theory came two important observations. The first was that the capacity of populations to evolve in response to selection can be limited by lack of genetic diversity (Chapter 9). The second was that genetic processes in small populations can reduce reproduction and survival, including resistance to disease (Chapters 9-10). An important step from there was to acknowledge that human activities affect evolutionary processes in natural populations as well as domesticates (Berry 1968; Frankel 1971,1974).

Another important contribution to Conservation Genetics was the use of genetics in wildlife management, particularly for harvested species (Figure 1.1). The development of allozyme electrophoresis as a robust method for screening genetic variation in natural populations allowed managers to identify discrete stocks and investigate the effects of harvesting, captive propagation and translocations on the genetic composition of these (e.g., Ryman et al. 1981; Ryman and Utter 1987). Analyses of phenotypic variation in heavily harvested species also lead to the realization that human activities constituted a powerful evolutionary force that was affecting the gene pool of the targeted species (see Chapter 12). The analysis of the genetic basis of more complex phenotypic traits, including those of immediate relevance to survival and reproduction, was developed for agricultural applications and is increasingly being applied in evolutionary biology (Lynch and Walsh 1999). Despite the obvious relevance of such traits to management of populations, the use of quantitative genetics methods to analyze or monitor genetic diversity in threatened or managed populations has been limited compared to molecular approaches. However both the concepts and

tools of quantitative genetics are increasingly relevant and accessible (Lynch 1996; Frankham 1999a), particularly for monitoring fitness-related traits (Chapter 3).

Both agricultural genetics and wildlife management, combined with studies of genetic (allozyme) and phenotypic variation in natural populations, therefore contributed to the focus on conserving genetic diversity as a primary goal of conservation genetics. But the allozyme analyses were also a fore-runner of the use of genetic markers to investigate population processes, such as paternity, mating system, population structure and gene flow, in threatened species subject to management. This field of "Molecular Ecology" developed rapidly in the 1990s as direct methods for detection and statistical analysis of variation in DNA were refined (Hillis et al. 1996; Goldstein and Schlotterer 1999; Nei and Kumar 2000, and see Chapter 2). Contributions of Molecular Ecology to practical conservation are now diverse and have broadened both the scope and relevance of Conservation Genetics. The refinements of methods for DNA analysis have also contributed to estimations of relationships among populations and species and approximate times of divergence among these; information that is finding increasing use in prioritizing taxa or areas for conservation effort (see Chapter 8).

The assessment of genetic diversity is also central to the contributions from systematics theory and practice to conservation genetics. Phylogenies represent estimates of deep genealogy that, under certain assumptions (see Chapter 8; Humphries et al. 1995), can act as a surrogate for overall feature diversity (Faith 1992). Thus, several methods have been proposed for prioritizing combinations of taxa or areas according to the phylogenetic breadth that they represent (Vane-Wright et al. 1991; Crozier 1997), though debate continues on the extent to which extinction reduces phylogenetic diversity (Nee and May 1999; Purvis et al. 2000; Hward and Mooers 2000). Phylogenies, especially those based on molecular characters (as a surrogate for time), can be used to examine the long-term tempo and geographic context of speciation and extinction (Barrowclough and Nee 2001; Nee 2001), which is of some relevance to current conservation (Moritz 1995; Harvey 2000). Phylogenies also form the basis of comparative approaches to assessing ecological correlates of extinction risk (Owens and Bennett 2000). Systematics also contributes more fundamentally through establishing formal taxonomy and, along with evolutionary theory, shaping views on one of the most vexing questions of all – what is a species? (Endler 1987; Cracraft 1998; DeQuiroz 1999; Hey 2001; see also Chapter 8).

Scope of Conservation Genetics

Conservation actions and the research necessary to support these should be targeted at multiple levels, including landscapes, ecosystems species and populations (Noss 1990). Conservation genetics focuses naturally at the population and species levels of organization, although applications to area/habitat-based management are becoming more prominent (Figure 1.1; Box 1.1). This focus makes sense in that species and populations are fundamental units in both ecology and evolution, making their management an essential contribution to conservation, but does not deny the fact that management of both habitats and populations is necessary to achieve a positive conservation outcome.

In the same sense, genetic and ecological approaches to population management should be seen as complementary and inextricably linked (Soule and Mills 1992; Hedrick et al. 1996; Box 1.1). On one hand, demographic variables such as sex ratio and variance in reproductive success are key determinants of rates of genetic processes within populations (see Chapter 5). On the other, genetic processes, e.g., inbreeding or genetic drift, often have substantial effects on key demographic variables such as fecundity and survivorship (see Chapters 9 and 10) and alone or through synergistic interactions with other stochastic processes can affect short-term population viability (Figure 1.2; Mills and Smouse 1994). It is also conceivable that genetically impoverished or inbred populations are more susceptible to some agents of decline, including disease and physical stress (Chapter 9)

The ecologist G. E. Hutchinson referred to ecological processes as "a series of ecological plays in an evolutionary theatre". This metaphor was developed for conservation biology by Meffe and Carroll (1994) who pointed out that we should be concerned about both the integrity of ecological systems as well as maintaining the capacity for evolution. The same applies to conservation genetics. Our goal is to use genetic tools and concepts, *together with ecological approaches*, to retain genetic and demographic processes in the short term and evolutionary processes in the long term. In practice, it is rare that management priorities based on genetic diversity conflict directly with those identified with ecological or demographic issues in mind. More often, there may just be a change in emphasis or, perhaps a broader justification for management strategies, particularly when planning for longer-term viability of populations and systems. (Table 1.1; Box 1.1).

The linkage between genetic and ecological approaches to management of populations is illustrated nicely by recent observations on recovery of the greater prairie chicken (*Tympanuchus cupido pinnatus*) in south-eastern Illinois (Figure 1.3; Westemeier et al. 1998). Declines in population size and productivity were observed over 35 years due to loss and fragmentation of habitats. Ecological management to restore the quality of critical grassland habitats led to a transient recovery in the early 1970s, but egg hatch rates and population size continued to decline until the loss of genetic diversity due to small population size and isolation was reversed by augmentation from large populations in the 1990s. In this case, both ecological and genetic issues needed to be addressed to achieve population recovery. Similarly, recent successes in management of the imperiled florida panther (*Felis concolor*) have required attention to both habitat protection and amelioration of inbreeding depression (see Chapter 11).

These and other examples reviewed in the following chapters reinforce our view that conservation genetics should not be seen as a distraction from the important issues in management, or even as something relevant only to the death rattle of small populations (Lande 1988; Caughley 1994; Caro and Laurenson 1994) but, rather, as a set of concepts and tools that should be brought to bear if and when appropriate. A major purpose of this book is to provide managers and practitioners with the background to decide when this is so.

The supposed separation of genetics and ecology in conservation also ignores the contribution that molecular genetic techniques can make to assessing the demography of threatened populations. The increasing use of the concepts and tools of Molecular Ecology in the study and management of endangered species (see below) have broadened the scope of Conservation Genetics such that the distinction between genetics and ecology is illusory. We therefore agree with Soule and Mills (1992) that, rather than wasting time and effort arguing about whether genetics is more important than ecology, we should get on with the job of conserving and restoring populations and habitats, using tools and concepts from genetics where appropriate.

From the above, it should be clear that we regard Conservation Genetics as having two major and complementary foci - the traditional domain of conserving genetic diversity, and the more recent development and application of Molecular Ecology (Moritz 1994a). The first area; “**Genetic Conservation**” has, as its central concerns:

1. Description of the amount and distribution of genetic diversity within species and evolutionary diversity among species;

2. Retention of variation within and among populations in order to maintain current fitness and long-term evolutionary potential; and
3. Avoidance of increases in inbreeding levels, especially in normally outbred species.
4. Development of methods to monitor effectiveness of management in relation to 1-3 above

The rationale for these activities was described by Franklin (1980) and Frankel and Soule (1981) and the pertinent evidence is reviewed in Chapters 8 to 10. Of particular importance is the development of efficient methods for monitoring genetic diversity and processes – without this, the need for, and effectiveness of management cannot be assessed. Yet, monitoring has been a weak link in the science of conservation genetics. In relation to genetic diversity, there has been justifiable criticism of the focus on “neutral” molecular variation when it is variation at the genes that underlie fitness that is crucial (Hedrick 1996; Lynch 1996; see Chapter 3). Throughout this book we will seek to identify ways in which relevant genetic diversity can be monitored via either direct measures, sometimes derived from new approaches in quantitative genetics or genomics, or surrogates. Monitoring of population parameters relevant to genetic processes, especially population size, migration, individual fitness and mate choice, benefits directly from the development of Molecular Ecology (Chapters 4-7).

The second focus of Conservation Genetics, "**Molecular Ecology**" combines the tools of molecular genetics with theory from population genetics to make inferences about individuals and populations (Hoelzal & Dover 1991; Avise 1994). The techniques and applications are diverse and typically are best applied in conjunction with detailed studies of population ecology (see chapters 4-7 for details). In many cases, the parameters estimated by genetic methods are prohibitively difficult to obtain using ecological methods alone. In others, the genetic approach provides a unique long-term perspective against which current population trends can be compared.

In the context of conservation and management, some of the more prominent applications of Molecular Ecology are:

1. Remote identification of individuals in species that are difficult to capture;
2. Analysis of parentage and related variables (e.g., variance of reproductive success) in closely managed populations; Estimation of short and long-term effective population size as an indicator of genetic processes within populations;

3. Identification of reproductively discrete populations (= Management Units, Moritz 1994b) or, for continuously distributed populations, the geographic scale over which exchange of individuals is trivial;
4. Estimation of rates of gene flow and detection of changes in migration patterns or metapopulation structure in modified landscapes; and
5. Detection of hybridization, e.g., between introduced species and remnant populations.

As discussed in Chapters 4-7, several of these applications (notably 3-5) often rest on assumptions that may not be satisfied for fluctuating populations, as is the case for most threatened species, so that the inferences from genetics are best compared to those from ecology.

In some respects the distinction between these two domains of Conservation Genetics is blurred. For example, the molecular ecology approach may be used to estimate the incidence of inbreeding or migration, both processes central to maintaining genetic diversity. Conversely, changes in levels of inbreeding, essentially a genetic process, may well affect the demographic parameters being estimated.

Nonetheless, we feel that the distinction is a useful one as the conservation goals and time-scales of concern are distinct, and in some respects, so are the techniques and sampling design (Moritz 1994a). Conservation of genetic diversity is primarily a long-term concern, although in some cases increased inbreeding or loss of genetic diversity may have an impact on short-term population viability. By contrast, the Molecular Ecology applications tend to be more focused on immediate ecological and demographic issues that are likely to be considered important whether or not the genetic and evolutionary issues are acknowledged.

An evolutionary perspective on conservation

It is an inescapable fact that the human species has caused long running and profound modifications to species diversity, the landscape, and environmental conditions (Figure 1.4) and may have done so for a long time (P.S. Martin 1973; Roberts et al. 2001). What is only now becoming appreciated is the extent to which human activities may be redirecting evolution (Myers and Knoll 2001). While the details are speculative (Figure 1.5), it is clear that evolution has not stopped; rather its rate and trajectory has been modified. Of particular concern are predictions that speciation of large vertebrates has ceased, that commensal species will dominate future radiations,

and that a drop in net speciation rate (speciation minus extinction) combined with reduced immigration means that already alarming predictions of species loss are underestimates (Rosenzweig 2001). In this context, Frankel's (1974) urging that we recognize and act on our responsibility as stewards of the evolutionary process becomes all the more relevant and urgent. This means coming to terms with conservation in a changing world (Balmford et al. 1998) and giving more attention to processes.

Given that humans are part of the environment and exercise profound influence on that environment, there is a fundamental decision that must be made in conservation efforts. This is whether we should either:

A) try to retain all taxa and phenotypic variants and restore ecosystems to unmodified conditions; or

B) accept that landscapes and broader environmental conditions are grossly modified and seek to maximize biological diversity within ecologically rehabilitated systems.

We feel that the latter, sometimes referred to as "countryside biogeography" (Daily et al. 2001) or "reconciliation ecology" (Rosenzweig 2001) is the only course that will permit the maintenance of ecological and evolutionary processes. We must acknowledge that humans have affected these processes and will continue to do so. To seek to return to an unmodified environment is not only unrealistic, but also represents a static view of biological diversity. What we can seek to do is maximize the extent to which natural evolutionary processes are retained.

The distinction between *conserving* ecological and evolutionary processes versus *preserving* the products, at the extreme the complete current array of distinct species and phenotypes, is an important one. As biologists we stand in awe of the products of evolution and lament the loss of any one. But, from an evolutionary perspective, we recognize that specific phenotypes and even species are ephemeral, one form replacing another as evolution proceeds. The challenge we face is not to retain all distinct populations, but rather to maintain sufficient diversity at the gene, species, and ecosystem levels to ensure that the underlying ecological and evolutionary processes continue.

This shift of emphasis from the products of evolution to the processes that sustain diversity has direct implications for planning and management. At the level of broad scale planning for biodiversity conservation (Chapter 8), landscape elements thought to be significant for diversification and evolutionary or ecological processes need to be included in algorithms for prioritizing areas (Moritz 2001; Cowling & Pressey 2001). When prioritizing species or populations for protection or management, consideration needs to be given to their level of phylogenetic distinctiveness (Vane-Wright et al. 1991) and whether the variation that they represent is likely to be recoverable through evolution (Chapter 8). For management of threatened species, an evolutionary approach can expand options, for example, in relation to augmentation or translocations of populations (Moritz 1999; Chapter 11).

Conservation genetics: an evolving science

Like most of conservation biology, Conservation Genetics is a young science still finding its way as established theory is put into practice and new tools and concepts arise. One of the exciting challenges is that applying theory and principles derived from laboratory studies and domesticated species to natural populations is revealing new insights and forcing the development of new theory. Examples of this include the dependency of effects of inbreeding and outbreeding depression on the condition of the environment (Chapters 10 and 11) and the development of methods to detect population bottlenecks and of non-equilibrium approaches to estimating population parameters from molecular data (Chapters 4-7). There are many others throughout this book.

Conservation genetics therefore encompasses fundamental as well as applied research. Indeed, as is usually the case, the distinction between fundamental and applied research is false. There should be, and is, a continuing process of adapting existing theory to natural populations and environments and this requires use of model systems and further laboratory studies (Frankham 1999), as well as experiments in the field.

An important part of the nexus between the refinement and application of conservation genetics is the use of "management experiments". Rather than the genetics being conducted in remote laboratories with the results being "presented" to the conservation managers, there is much to be gained from direct involvement by geneticists in ongoing management and, conversely, by involvement of the managers in

the genetic research and monitoring (Sherwin & Moritz 2000). This ensures that the genetics is integrated into parallel ecological studies and that genotype or environment specific effects of genetic processes are appropriately measured. It also helps to establish mutual understanding between conservation managers and geneticists, allowing the former to appreciate the strengths and limitations of genetics and, the latter, the practical issues that need to be addressed (Moritz et al. 1994).

This book is intended to contribute to the defining of Conservation Genetics as a discipline and enhancing its relevance to practical management of populations, species and habitats. The success or otherwise of the book should be judged by the extent to which it informs the day to day thinking of a conservation manager or stimulates both fundamental and applied research by present and future students. Towards this end, we review current theory, experimental evidence and examples of the application of genetics to practical conservation. This identifies areas of current strength and limitation, key research questions, and ways of approaching them. We first introduce the analytical and experimental tools (Chapters 2 - 3), then consider the theory and its applications in the areas of molecular ecology (Chapters 4 - 7) and conservation of genetic diversity (Chapters 8 - 12). The concluding chapter (Chapter 13) provides a guide to managers on how to link the theory and tools of conservation genetics to specific problems in conservation and reviews future prospects and directions for Conservation Genetics.

Summary

1. Conservation Genetics was born of concern about erosion of genetic resources and the impact of humans on the evolutionary process. It has been strengthened by the use of molecular biology techniques to describe biological diversity and to provide insights into evolutionary and ecological processes.
2. The central concern of conservation biology is to maximize biological diversity in the short and long term. This requires that we maintain and, as far as possible, restore ecological and evolutionary processes.
3. Conservation Genetics contributes to this goal through two, non-exclusive areas of activity: (i) conservation of genetic and evolutionary diversity, and (ii) molecular ecology, the use of molecular techniques to investigate ecological processes. In practice, Conservation Genetics is most powerful when it

complements, rather than replaces, traditional approaches in systematics and ecology, and is fully integrated into recovery planning.

4. Conservation strategies and management need to recognize the extent to which humans have modified the evolutionary process and our responsibility as stewards of evolution. Our approach to conservation of habitats and populations should therefore be informed by an understanding of historical and current processes that sustain biological diversity..
5. Conservation Genetics is at an exciting stage of its development as principles derived from theory and laboratory studies are applied to natural systems. Further theoretical and experimental studies, the latter using both model systems and "management experiments" conducted as part of recovery actions, are needed for Conservation Genetics to become a more predictive science with practical benefits.

Tables and figures

Figure 1.1 Schematic history of Conservation Genetics – contributing disciplines

Figure 1.2 – Extinction vortex – interaction of genetic and demographic processes
(from Gilpin & Soule)

Figure 1.3 prairie chickens – complementary habitat and genetic management –
modified from Westemeier et al. 1998

Figure 1.4 - a) rates of physical changes - temp or atmospheric CO₂; b) rates of biotic
change – introductions of fish to USA nico & Fuller 1999; c) global biodiversity
hotspots Myers et al. 2000, Cincotta et al.; d) projections – Sala et al. 2000

Figure 1.5 – changes in evolutionary processes – from Myers & Knoll 2001

Table 1.1. Ten intersecting questions from ecologists and geneticists compared

Ecologists

Local issues:

- Is the population increasing or decreasing?
- If decreasing, what cause(s) can be identified and what aspect of the life cycle has the strongest effect on changes in population size?
- Does the species depend on specific habitat types or interactions with other species that have been disrupted by human activities?
- What management activities have the best chance of restoring population viability?

Regional issues:

- Has connectivity among populations been reduced such that metapopulation viability is threatened?
- What proportion of the species range is threatened to otherwise impacted by human activities?

Geneticists

Local issues:

- Has the population sufficient genetic diversity to respond to selection?
- Is there evidence for inbreeding depression?
- Has there been a recent decrease in genetic diversity or increase in inbreeding attributable to human activity?
- Is the population accumulating disadvantageous mutations because of reduced population size or increased isolation?
- Has the genetic makeup of the population been changed by hybridization with introduced species or populations?

Regional issues:

- Has gene flow among populations been changed (typically, decreased) by human activities?
- Have genetically divergent populations been lost across the species' range?

Box 1.1 Comparison of parameters relating to process and pattern and of concern to managers, ecologists and geneticists

Level	Manager	Ecologist	Geneticist
Ecosystem			
• processes	Extent/frequency of Fire & weeds; erosion, water quality	Energy & nutrient cycling; vegetation succession	Coevolution of interacting species
• pattern	Number/status of vegetation types	Alpha, beta, gamma diversity of species; habitat configuration	Retention of historically isolated communities
Species			
• processes	Species viability within jurisdiction	Demography: $l_x m_x$ etc; PVA	Gene flow and population structure
• pattern	Changes in numbers of EVRs; population trends	Population trends; area occupied	Phylogenetic diversity
Genes			
• process	Population size & inbreeding	Mate choice and availability, adaptability	Rate of genetic change and inbreeding
• pattern	Heterozygosity?	Physiological tolerances, morphological and life history traits	Heritability, heterozygosity, genetic diversity among populations

Figure 1.1 Schematic history of Conservation Genetics- contributing disciplines

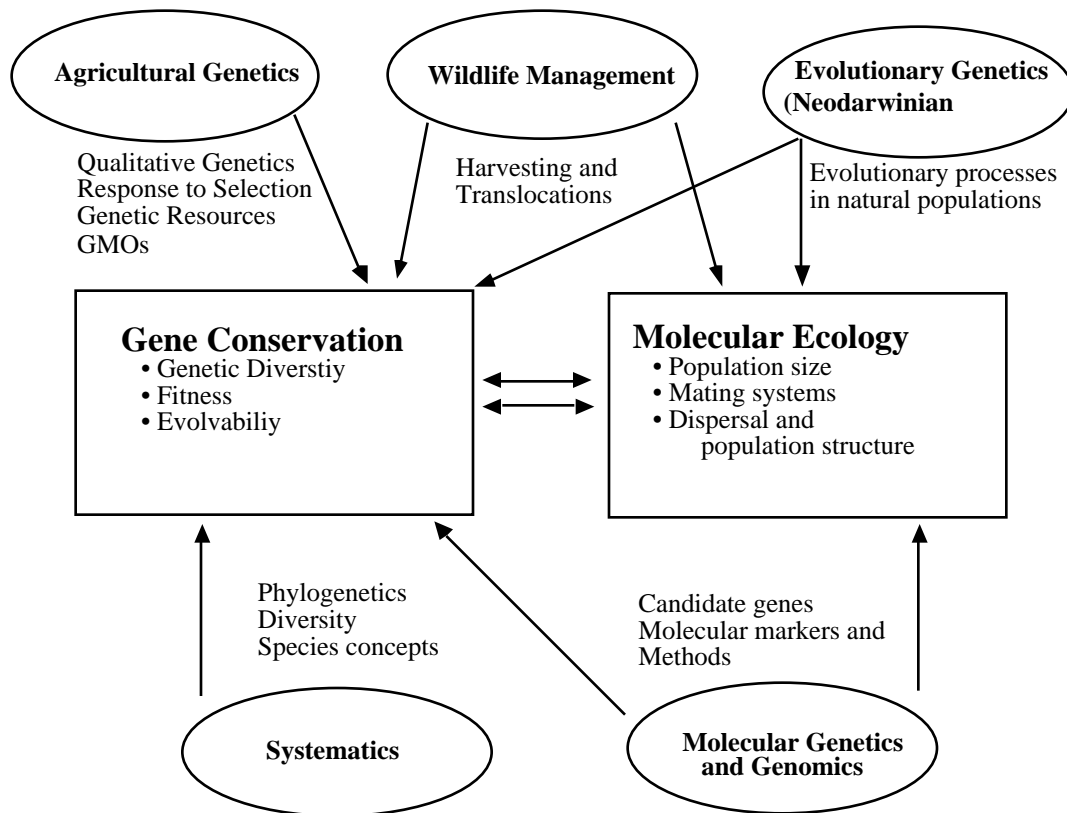


Figure 1.2 Extinction vortex- interaction of genetic and demographic processes (from Gilpin and Soule 1986)

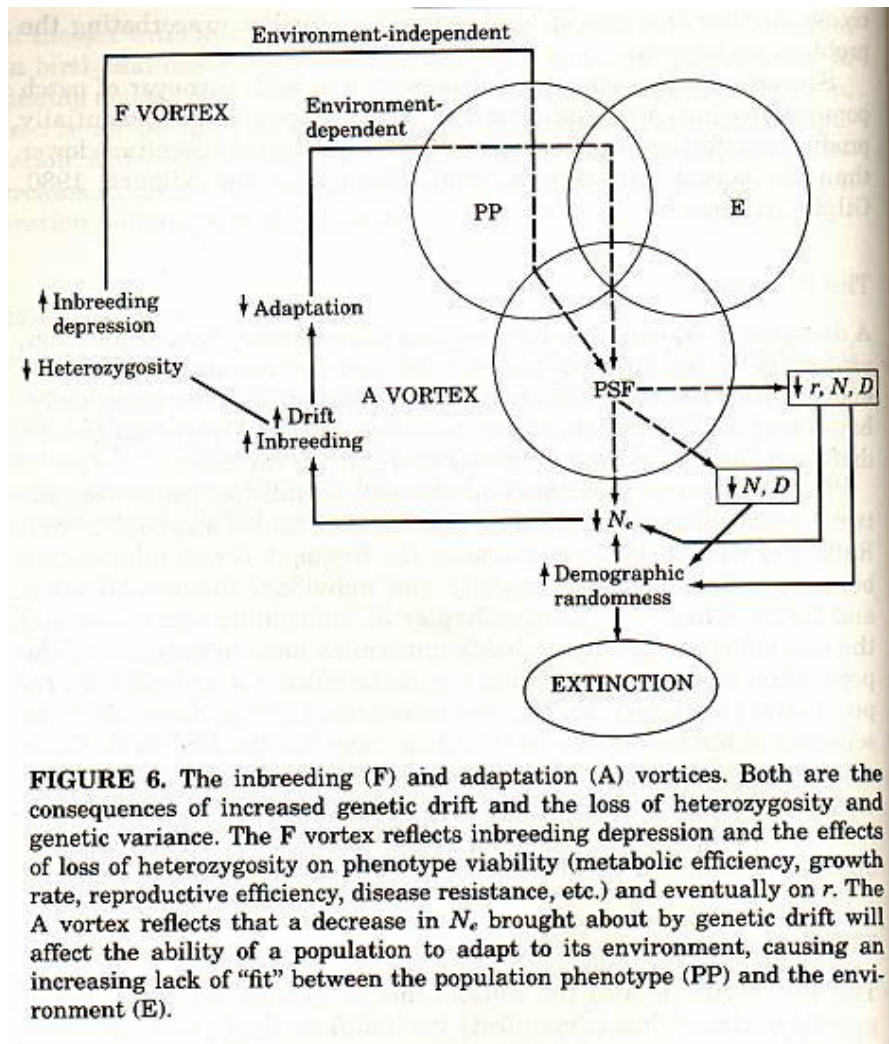


FIGURE 6. The inbreeding (F) and adaptation (A) vortices. Both are the consequences of increased genetic drift and the loss of heterozygosity and genetic variance. The F vortex reflects inbreeding depression and the effects of loss of heterozygosity on phenotype viability (metabolic efficiency, growth rate, reproductive efficiency, disease resistance, etc.) and eventually on r . The A vortex reflects that a decrease in N_e brought about by genetic drift will affect the ability of a population to adapt to its environment, causing an increasing lack of "fit" between the population phenotype (PP) and the environment (E).

Figure 1.3 Complimentary habitat and genetic management in prairie chickens (from Westemeier et al. 1998)

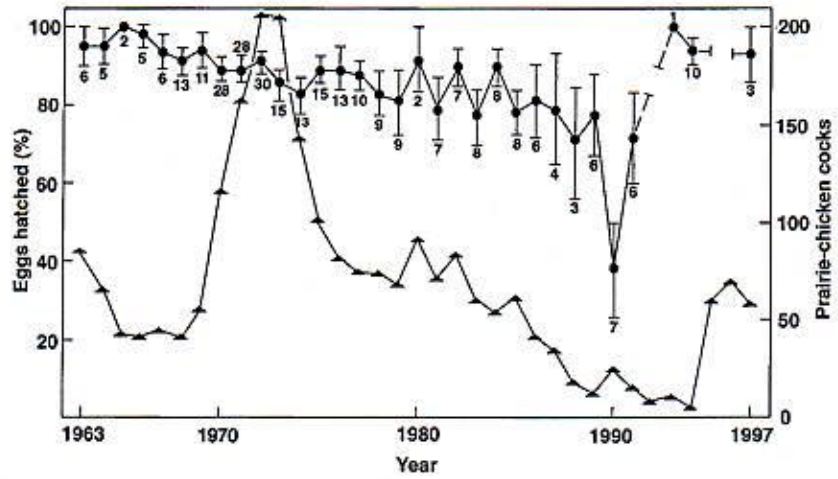


Fig. 2. Annual means for success of greater prairie chicken eggs in 304 fully incubated clutches (circles) and counts of males (triangles) on booming grounds in spring, Jasper County, Illinois, 1963–1997. Translocations of nonresident birds began in August 1992. Test statistics (24) for the period 1963–1991 are as follows: egg success rates, $\phi = 4.28$ ($P < 0.001$); male counts, $\phi = 1.88$ ($P = 0.0301$). Bars indicate ± 1 SE and adjacent numbers indicate numbers of nests. For egg fertility rates (not shown), $\phi = 2.18$ ($P = 0.0146$).

Figure 1.5 Possible changes to the direction and rate of evolution wrought by human impacts of the environment. Drawn from Myers and Knoll (2001) and Woodruff (2001).

