
The History, Purview, and Future of Conservation Genetics

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Direct and indirect effects of human population growth are precipitating sharp declines of biodiversity worldwide. The field of conservation biology has been defined as “a response by the scientific community to the biodiversity crisis” (Meffe & Carroll, 1997, p. 4). Biodiversity *is*, ultimately, genetic diversity, a product of evolutionary processes. Thus, the field of conservation genetics could be defined as “a response by the scientific community to the genetic diversity crisis.” However, any definition this broad is unduly vague and fails to convey what practicing conservation geneticists actually do. At the other end of the spectrum, conservation genetics has sometimes been portrayed as a discipline devoted mostly to problems associated with inbreeding and the loss of adaptive genetic variation in small populations. However, any definition this narrow is unduly restrictive.

Perhaps a more useful approach is to define conservation genetics as the study of genetic patterns or processes in any context that informs conservation efforts. Theoretical population genetics and phylogenetics, as well as molecular and other empirical studies of genetic patterns and processes in captive and natural populations, have all played key roles in the emergence of conservation genetics as a recognizable subdiscipline of conservation biology. My goals in this review are the following: survey the extensive scientific literature that self-describes as being in the realm of conservation genetics; categorize major research themes within

this field; comment on past accomplishments and future prospects with regard to each of those primary themes; and, lastly, outline a panorama of the burgeoning field of conservation genetics in the broader framework of conservation biology.

A BRIEF HISTORY OF CONSERVATION GENETICS

Before the 1960s, genetic properties of most species could be inferred only indirectly (and rather insecurely) via descriptions of organismal phenotypes such as morphologies and behaviors. Since then, a succession of powerful molecular technologies has given researchers direct access to voluminous genetic information stored naturally in nucleic acids and proteins. Patterns of genetic diversity within and among individuals, kinship groups, populations, species, and supraspecific taxa can now be investigated using molecular genetic data in addition to phenotypic traits. As this book attests, conservation biologists now incorporate genetic appraisals routinely in studies of plant and animal mating systems; behavior and natural history; population structure resulting from past and present demographic factors; gene flow, genetic drift, and selection; speciation, hybridization, introgression, phylogeny, systematics, and taxonomy; forensic identification of wildlife and wildlife products; and many additional topics relevant to conservation

TABLE 1.1 Some Historical Milestones in Conservation Genetics*.

1966	Lewontin and Hubby introduce allozyme methods to population biology.
1973	The U.S. Endangered Species Act sets a legal precedent to save rare taxa.
1974	Frankel publishes an article on genetic conservation as an evolutionary responsibility.
1975	Frankel and Hawkes edit a volume on genetic resources in crops. Martin edits a book on the captive breeding of endangered species.
1979	Ralls, Bruggler, and Ballou draw attention to inbreeding depression in captive demes. Avise and colleagues as well as Brown and Wright introduce mtDNA methods to population biology.
1980	Soulé and Wilcox publish the first of several conservation books with an evolutionary genetic as well as ecological orientation.
1982	Laerm and colleagues publish perhaps the first multifaceted genetic appraisal of a wild, endangered species.
1983	Schonewald-Cox and colleagues edit the first major book on conservation and genetics. O'Brien and colleagues initiate studies on inbreeding effects in wild felids. Mullis invents polymerase chain reaction (PCR) for in vitro amplification of DNA.
1985	The Society for Conservation Biology is formed. Jeffreys and colleagues introduce multilocus DNA fingerprinting methods.
1986	Ryder brings the phrase <i>evolutionarily significant unit</i> to wide attention.
1987	Ryman and Utter edit a book on population genetics in fishery management. The journal <i>Conservation Biology</i> is launched. Avise and colleagues coin the term <i>phylogeography</i> and outline the field.
1988	Lande distinguishes genetic from demographic issues in small populations.
1989	The Captive Breeding Specialist Group initiates "population viability analyses" for endangered taxa. The U.S. Fish and Wildlife Service opens a wildlife forensics lab in Ashford, Oregon. Tautz (among others) introduces microsatellites as a source of polymorphic nuclear markers.
1990	Hillis and Moritz edit a book on molecular approaches to systematics.
1991	Vane-Wright and colleagues raise issues about phylogenetic diversity and conservation worth. Falk and Holsinger edit a volume on conservation genetics in rare plants.
1992	Avise introduces a regional phylogeographic perspective to conservation. Hedrick and Miller discuss genetic diversity and disease susceptibility in conservation. Groombridge edits a taxonomic and genetic inventory of global biodiversity.
1993	Thornhill edits a book on the natural history of inbreeding and outbreeding.
1994	Avise publishes the first major textbook on molecular genetic approaches in ecology, evolution, and conservation. Loeschcke, Tomiuk, and Jain edit a volume on conservation genetics. Burke edits an issue of <i>Molecular Ecology</i> on conservation genetics.
1995	Ballou, Gilpin, and Foose edit a book on genetic and demographic management of small populations.
1996	Avise and Hamrick as well as Smith and Wayne edit books on molecular approaches to conservation genetics. O'Brien initiates a biannual conservation genetics course, sponsored by the American Genetic Association and Smithsonian, that has trained many conservation geneticists.
1997	Hanski and Gilpin edit an important volume on metapopulations.
1998	Allendorf edits an issue of <i>Journal of Heredity</i> on conservation genetics in the sea.
1999	Landweber and Dobson edit a volume on genetics and species extinction. Wildt and Wemmer address reproductive technologies in conservation biology.
2000	The journal <i>Conservation Genetics</i> is launched. Avise publishes the first textbook on phylogeography.
2002	Frankham, Ballou, and Briscoe publish the first "teaching textbook" on conservation genetics.
2005	Purvis, Brooks, and Gittleman edit a book on phylogeny and conservation.

*With all due apologies to numerous additional authors whose works could justifiably have been cited as well. See Meffe and Carroll (1997) for a history of the broader field of conservation biology.

efforts. Conservation genetic studies are often targeted on particular populations or species that are imperiled, but they can also be aimed at composite biotas or comparative themes, or toward uncovering conservation lessons from species that are not currently in danger of extinction.

The formal birth of conservation genetics occurred with the publication in 1983 of *Genetics and Conservation*, edited by Schonewald-Cox and colleagues. This nascent discipline had emerged from the well-established conceptual frameworks

of population genetics, ecological genetics, quantitative genetics, evolutionary genetics, and phylogenetics, as now applied to biodiversity issues. Conservation genetics in 1983 was not a tightly knit field, but rather an ensemble of genetic approaches loosely united by a shared relevance to conservation efforts. I think that the same can be said of this eclectic field today.

Table 1.1 summarizes many of the milestone events, both before and after 1983, in the history of conservation genetics. Several breakthroughs

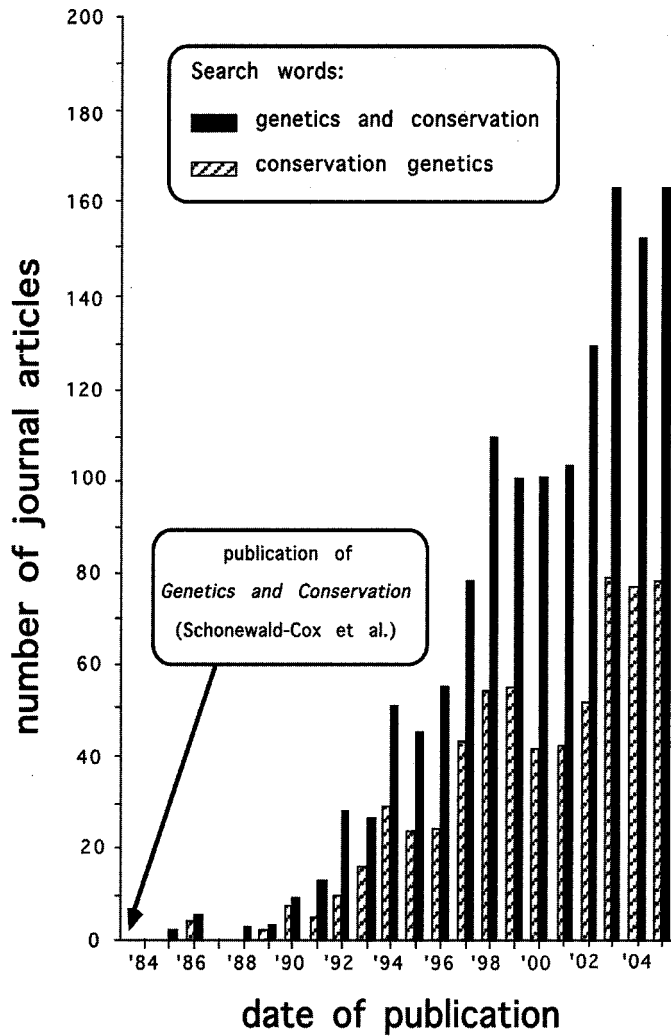


FIGURE 1.1 Number of conservation genetics articles (as identified in computer searches using the indicated key words) published from 1983 to 2006.

involved introductions of laboratory methods for revealing molecular genetic variation, followed by pioneering applications of each technique to conservation or management. Other landmark publications involved the introduction of key concepts to conservation genetics, journal reviews, edited volumes, and authored textbooks.

To quantify how the field of conservation genetics has grown since 1983, and to assess what its practitioners mean when they use the words conservation and genetics jointly, late in the year 2006 I conducted a search of the scientific literature. I used the computer database available

at <http://isiwebofknowledge.com> and searched the terms genetics and conservation joined by the Boolean operator *and*, along with the operator-free search term conservation genetics. Figure 1.1 shows a temporal breakdown of the nearly 2,000 articles identified. These papers represent only a fraction of the genetics literature relevant to conservation, but they nonetheless provide a useful guide to the historical trajectory and to the traditionally perceived scope of the discipline.

After a lag in the 1980s, the number of conservation genetic publications per year has grown

dramatically and consistently. The impact of molecular biology on the field is evidenced by the fact that approximately two thirds of all publications centered on analyses of protein or DNA data. The remaining studies that emerged from the computer searches involved conservation-relevant genetic theory, or empirical conservation assessments based on other data such as species lists, phenotypes, or biogeographic patterns.

MAJOR CONSERVATION GENETIC THEMES

The literature searches also provided an opportunity to identify and quantify research foci in conservation genetics. Many topical breakdowns are possible; I arbitrarily chose to categorize publications into the five primary subject areas pictured in the top half of Figure 1.2 What follows are some brief comments about each of these topics.

Variation within Populations

History and Purview

About 25% of journal articles found with the search term conservation genetics focused on genetic issues within small captive or natural populations. Loss of genetic variation under inbreeding—the result of mating among genetic relatives—was the most common theme in these articles, but a smaller number of studies addressed three related areas of research: the longer term demographic history of a single population as deduced by, for example, coalescent theory; parentage, kinship, or gender identification of relevance to captive breeding programs; or the microspatial dispersal of organisms in the context of natural history, reproductive modes, and mating systems in nature.

Deleterious effects of inbreeding have been understood for centuries (Darwin, 1868), and the genetic causes and consequences of inbreeding depression remain important research topics today (Brook, this volume; Hedrick & Kalinowski, 2000). For example, susceptibility to inbreeding depression has been quantified in many empirical studies, and the avoidance of inbreeding depression has been a major goal in the design of captive breeding programs and the management of small or isolated natural populations.

Many of the earliest studies identified in my literature searches addressed theoretical and empirical

effects of inbreeding (and outbreeding) on fitness components such as viability and fertility. And following the introduction of molecular tools for population biology, the consequences of inbreeding could also be evaluated in terms of diminished heterozygosity at specific loci. This technological advance in turn led to the widespread use of multilocus molecular data (for example, from allozymes or microsatellites) to quantify genomic variation, which was sometimes used as a measure of population genetic “health,” or adaptive potential.

These interpretations were prompted by reports of a positive correlation between heterozygosity and traits associated with enhanced reproduction, such as growth rate or disease resistance (Mitton, 1997). For several reasons, however, caution is indicated in concluding that observed levels of molecular variation predict population viability (Hedrick, 2001). One problem is that studies that show positive correlation between heterozygosity and fitness are more likely to be published than those showing a non-significant correlation, resulting in a publication bias. A second problem is that many molecular studies have been based on too few loci to rank order individuals (or even populations) reliably by heterozygosity. And lastly, magnitudes of variation in molecular markers often correlate poorly with quantitative genetic variation that is more likely the target of natural selection and thus the product of adaptive evolution (Reed & Frankham, 2001).

Representative Examples from the Literature Search

Laikre (1999) demonstrated high genetic load and severe inbreeding depression in zoo-maintained populations of brown bears, gray wolves, and lynx. A similar result was found by van Oosterhout and colleagues (2000) for captive populations of a butterfly species that is normally outbred in the wild. Authors of both studies discussed the ramifications of such findings for population management.

Frankham and colleagues (2000) revisited a longstanding theoretical prediction from quantitative genetics. Theory suggests that equalization of family sizes in controlled breeding programs should reduce genetic adaptation to captivity and thereby enhance prospects for successful reintroductions

Conservation Genetics

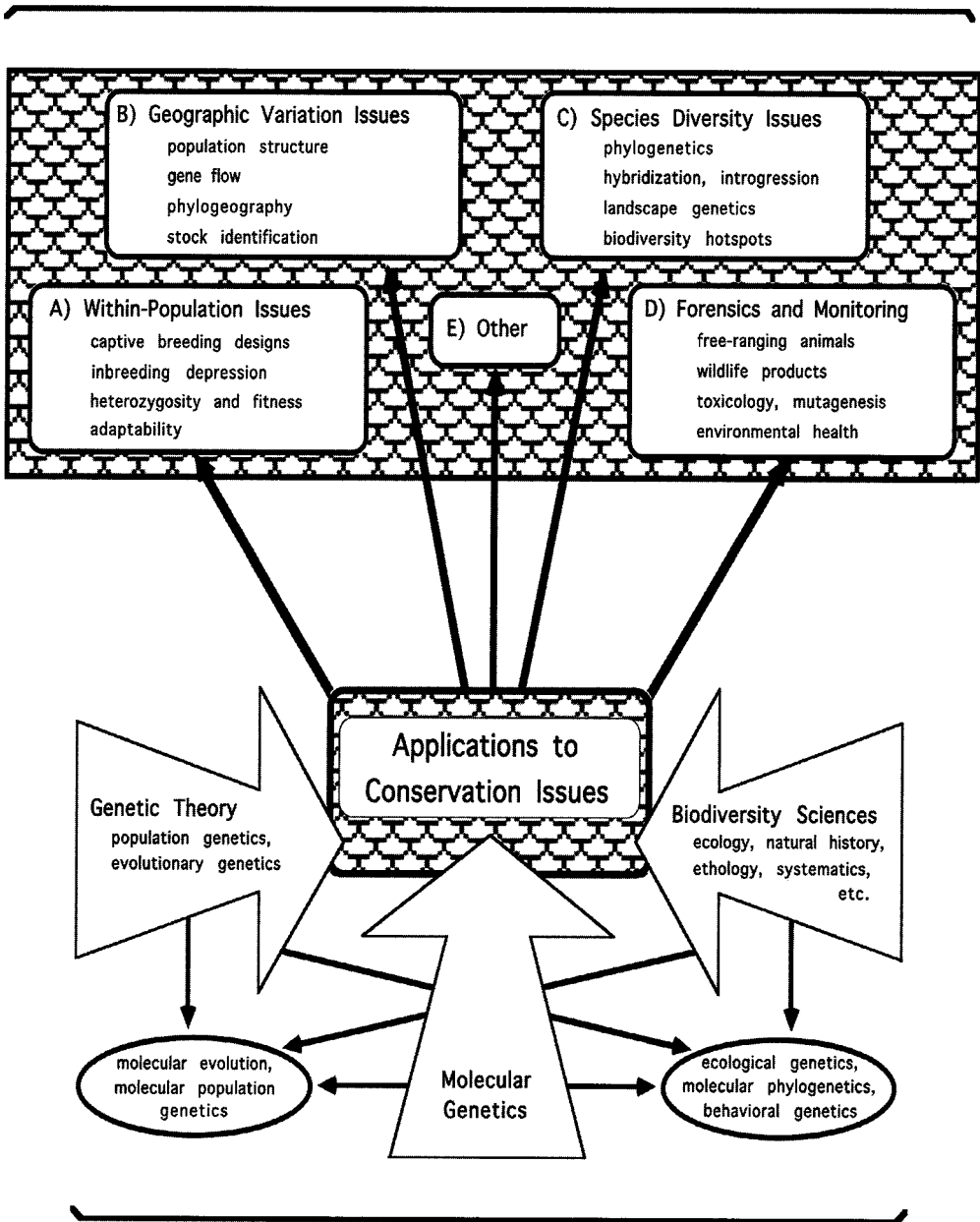


FIGURE 1.2 The purview of conservation genetics (upper half of figure), and the field's empirical and conceptual foundations within the time-honored life sciences (lower half of figure).

to nature. The authors cast doubt on the universality of this prediction when they showed that fruit flies raised for 25 generations under either equal or variable family sizes had similar reductions in reproductive success when returned to the wild. Armbruster and Reed (2005) reviewed the literature to test another outstanding prediction: Deleterious effects of inbreeding should be more evident in harsh environments than in benign environments. However, what they found was that inbreeding depression increased significantly under stress in only about 50% of the 34 studies they reviewed.

Other types of within-population assessments relevant to conservation are illustrated by the following studies. Spong and colleagues (2000) observed high heterozygosity at microsatellite loci in Tanzanian leopards. Using statistical inference, they concluded that the evolutionary effective population size was about 40,000 individuals, and that the number of leopards in this geographic region had been large and stable for several thousand years. In a different kind of intrapopulation conservation application, Sacchi and coworkers (2004) used sex-linked genetic markers to reveal the sex (otherwise unknown) of particular individuals in the endangered short-toed eagle.

Geographic Variation

History and Purview

Nearly 50% of conservation genetic articles in my literature searches involved comparisons among conspecific populations. These studies often addressed geographic population structure in particular species; spatial dispersal and gene flow, including both ongoing and historical patterns of genetic transfer among populations; genetic drift; or the delimitation of genetic and demographic stocks. Each analysis was typically conducted in the context of recognizing ecological and evolutionary sources of intraspecific genetic variation for conservation purposes.

Traditional population genetics and phylogeography were the two main areas of focus within this broader category of research. Papers in population genetics usually addressed geographic variation in allelic frequencies at allozyme or microsatellite loci, whereas studies of phylogeography often analyzed intraspecific gene trees of mitochondrial (mt) DNA. Although both these research programs seek

to illuminate the causes and consequences of spatial genetic patterns in nature, population genetics is primarily concerned with contemporary forces molding populations. In contrast, phylogeography evaluates historical genealogical processes. The most powerful empirical studies to emerge from my literature search incorporated elements of both methodological tool boxes, and utilized data from multiple nuclear and cytoplasmic genes.

An important distinction in conservation biology is between management units (MUs) and evolutionarily significant units (ESUs). By definition, MUs are populations that currently exchange so few individuals as to be, in effect, demographically independent from one another at the present time (regardless of how recent or extensive their prior historical genetic connections); ESUs, by contrast, are populations with long histories of genetic separation. All ESUs are potential MUs, but not all MUs are ESUs. Population genetic and phylogeographic analyses have both been extremely useful in identifying otherwise cryptic MUs and ESUs in hundreds of imperiled and other species. For detailed examples from this vast literature, readers are directed to a recent extensive review by Avise (2000).

Species Diversity

History and Purview

This broad category includes genetic studies dealing with issues at and above the species level of taxonomy. About 12% of the author-identified "conservation genetics" papers were of this type. Given that a much broader literature exists on speciation, hybridization, introgression, and molecular phylogenetics, the articles identified in my database search clearly represent only a small fraction of evolutionary studies with potential relevance to biodiversity assessments and conservation.

Representative Examples from the Literature Search

Demarais and colleagues (1992) used cytonuclear markers to document that an endangered fish in the American Southwest (*Gila seminuda*) is the product of introgression between *G. robusta* and *G. elegans*. Similarly, Aparicio and coworkers (2000) confirmed by molecular analyses that a Spanish population of endangered plant, *Phlomis* × *margaritae*, arose via interspecific crosses. In an

allied sort of conservation-relevant application, Ellstrand (2003b) reviewed evidence that most of the world's major food crops occasionally hybridize with wild relatives, a process that may compromise the genetic integrity of native progenitor species and perhaps even cause their introgressive extinction (in other words, genetic swamping [Rhymer, this volume; Rhymer & Simberloff, 1996]).

Outstanding issues regarding taxonomy and systematics have also been resolved. For example, Friesen and colleagues (1996) provided molecular evidence for elevating the taxonomic status of an endangered seabird to a full species. And in a similar vein, Hickson and coworkers (1992) used molecular genetics to justify splitting into separate species each of several morphologically cryptic forms of New Zealand skinks. With regard to phylogenetic patterns originating farther back in time, Bowen and colleagues (1993) discussed conservation ramifications of a molecular phylogeny for extant species of marine turtles, all of which are listed as threatened or endangered.

Considerable discussion has centered on phylogenetic distinctiveness as a measure of taxon "worth" when priority decisions are made regarding investment of finite time and conservation resources (Faith, this volume; Purvis et al., 2005). A basic notion is that unique (in other words, long-separated) evolutionary lineages contribute disproportionately to the planet's overall genetic diversity, such that their extinction would constitute a far greater loss of biodiversity than would the extinction of species that have extant close relatives. Although phylogenetic considerations can be important in particular instances, my own guess is that they will seldom override more traditional criteria used by societies to decide which species or biotas merit greatest protection (Avisé, 2005). These conventional ranking criteria (explicit or implicit) often include a species' inherent charismatic appeal to humans, its rarity or restricted distribution per se, or its ecological or economic significance.

Wildlife Forensics

History and Purview

About 5% of the studies uncovered in my literature searches used molecular genetics in forensic identification. Two contexts were paramount: censuses of free-ranging animals using genetic samples

collected from hair, feathers, skin, or feces; and ascertainment of the geographic source of confiscated wildlife products such as elephant tusks or rhinoceros horns. A great boon to forensic applications was the invention of the polymerase chain reaction (PCR), a relatively noninvasive molecular technique that permits in vitro amplification of specific DNA sequences from very small samples of tissue like that found in hair or a drop of blood.

Representative Examples from the Literature Search

In one study, Taberlet and colleagues (1997) used PCR-based analyses of microsatellite loci to determine the genotype of hair and feces from a wild population of endangered Pyrenean brown bears. Unfortunately, they concluded that the bear population consisted of just a few individuals. And Palsbøll (1999) reviewed applications and potential pitfalls to the use of molecular markers to "genetically tag" wild animals.

Illicit trade in animal products was investigated by Baker and colleagues (2000). These researchers used mtDNA sequences to identify protected cetaceans in commercially available stocks of whale meat. Similarly, Roman and Bowen (2000) showed with mtDNA markers that about 25% of "turtle meat" stocks in markets of Louisiana and Florida were incorrectly identified to source species.

Other Topics

Other studies captured in my database searches covered a miscellany of topics and genetic approaches that I could not easily pigeonhole into any of the aforementioned subject headings. For example, several papers examined in vitro maintenance of DNA banks, germplasms, or tissues, such as cryopreserved cells of endangered species (Ryder et al., 2000; Wildt et al., 1997). Another handful of distinctive papers explored the use of genetic markers as tools for monitoring mutagenic or other biological impacts of chemical toxins and pollutants. As examples, Street and colleagues (1998) assessed the genetic consequences of hydrocarbon spills on copepods, and Bickham and coworkers (2000) reviewed potential applications for population genetic data and models in the fields of biomonitoring and ecotoxicology.

To my surprise, the computer searches identified only a few articles involving genetic engineering in a conservation context. This gap in the literature is remarkable given the prominence of genetic engineering in arenas such as agriculture, animal husbandry, and environmental bioremediation (Awise, 2004b). Assessing the ecological or genetic costs and benefits of releasing genetically modified organisms into the environment (Wolfenbarger & Phifer, 2000) falls within the purview of conservation genetics. Similarly, a conversation-oriented perspective could be applied to engineering plant or animal species to carry, for example, transgenes that protect against pests or diseases (Adams et al., 2002). Although numerous such papers exist, they were seldom identified under the search term genetics *and* conservation.

Likewise, my targeted searches uncovered few “conservation genetics” articles involving methods of reproductive manipulation. These methods would include, for example, *in vitro* fertilization, artificial insemination, embryonic transfer, or organismal cloning. Again, this gap in the literature is surprising because many of these methods already are (and others may soon become) standard practice in captive breeding programs for endangered species (see, for example, Cohen, 1997).

Reproductive and genetic efforts often grade into one another. For example, more than 15 years of basic research into the refractory reproductive biology of cheetahs finally yielded successful techniques for artificial insemination using fresh or frozen-thawed sperm (Wildt & Wemmer, 1999). These methods in turn can be used in breeding programs to facilitate reproduction and to minimize inbreeding depression in this endangered cat.

FUTURE DIRECTIONS

Paradoxically, the field of conservation genetics will have ample room for growth as the world's biotas become increasingly stressed from the relentless pressures of human overpopulation. No crystal ball is needed to predict that as evolutionary lineages become increasingly threatened by human activities, conservation genetic studies will be expanded to many more populations, species, and higher taxa, as well as to additional ecological settings.

However, newly emerging molecular genetic technologies will offer unprecedented opportunities for exploring and understanding organismal

genomes in ways that are germane to the theory and practice of conservation biology. In the following sections (which mirror the five topical areas in Fig. 1.2), I briefly highlight what I believe are excellent opportunities for empirical and conceptual advances as biologists further enter the genomics era.

Local Kinship

Many standard molecular genetics assays can be brought to bear on a host of within-population assessments. For example, offspring parentage, mating systems, determination of individual sex, and identification of clonal lineages are the types of problems that are now routinely addressed with molecular genetic assays. However, other within-population applications are only poorly addressed by the kinds of methods currently in wide use. One area of much-needed improvement is in estimates of coefficients of relatedness for other than full-sibs or parent-offspring pairs. Most studies to date lack the statistical power to infer with confidence the relationships among nondescendent kin such as half-siblings, cousins, grandparents, and so forth. In the near future, far more comprehensive genomic scans might be accomplished with markers such as single-nucleotide polymorphisms (SNPs), which permit individuals to be genotyped for a very large number of independent loci. Hundreds or even thousands of independent molecular polymorphisms will soon be available for many model, and perhaps nonmodel, taxa. These markers should help considerably in refining empirical estimates of genetic relatedness and assist molecular ecologists in their understanding of behavior and other phenotypes.

Conspecific Populations

A major current challenge in the field of phylogeography (especially for proper ESU identification) is to increase the number of independent gene genealogies examined within particular species. For biological and technical reasons, most phylogeographic studies to date have focused on mtDNA, but this maternally transmitted molecule carries only a minuscule fraction of any population's total hereditary history, most of which is collectively recorded at nuclear loci. Thus, although the biological hurdles (for example, intragenic recombination) and technical hurdles (haplotype isolation) remain high

in many cases, in principle much stands to be gained by extending powerful genealogical appraisals to multiple nuclear loci.

Another challenge for the field will be to develop more realistic models that link current population genetic patterns to historical demographic processes. For reasons of mathematical tractability, much of traditional population genetic theory was built on equilibrium outcomes, but of course most natural populations are in continual or episodic flux in relevant parameters like population size and gene flow (see Reed, this volume). Phylogeographic perspectives (including coalescent theory and branching process models) have already moved population genetics toward greater realism by addressing some of the idiosyncratic, nonequilibrium demographic histories of particular populations and species. However, much remains to be accomplished, especially in developing a multilocus coalescent theory that tackles the expected variances across gene genealogies under alternative historical demographic scenarios. Hopefully, results of such theory could then be used to interpret genealogical data (analogous to those from mtDNA) that in the not-too-distant future might be gathered routinely in molecular surveys of large numbers of unlinked nuclear loci.

Supraspecific Issues

The genomics era will likewise offer—indeed, demand—information from many more loci in conservation applications that involve species and higher order taxa. For example, careful genomic study of large numbers of unlinked markers can provide important insights into variation in introgression patterns of natural populations, as well as illuminate the nature and frequency of horizontal gene transfer. Barriers to the hybridization-mediated exchange of genetic material between biological species are often semipermeable rather than absolute, but this phenomenon can only be revealed in multilocus assessments. Interspecific gene flow can affect organismal fitness, phylogenetic reconstructions, and species identifications, and in general be relevant to conservation efforts in many other ways.

Functional genomics is a vibrant branch of genetics that seeks to identify direct mechanistic links between genes and particular adaptations. Genes of the major histocompatibility complex, which influence resistance to pathogens and infectious disease, are just one example of loci in threatened

or endangered species with patterns of variation that can provide functional information relevant to conservation efforts.

As science further enters the genomics era, another exciting opportunity will be afforded: to reconstruct, once and for all, the Tree of Life. Ideally, this collective scientific effort should include robust estimates not only of branching topologies, but also of ancestral nodal dates estimated with a molecular genetic clock that has been integrated with traditional fossil and biogeographic evidence. At least for many major taxa and clades, this grand phylogenetic synthesis should be completed within the next two decades, and it will stand as one of the grand achievements in the history of biology. Conservation biology will benefit from this massive tree reconstruction effort because improved evolutionary road maps of biodiversity will assist efforts to protect threatened taxa.

Forensic Applications

The goal of DNA bar coding methodologies is to use large-scale taxonomic screening of one or a few reference loci to assign individuals to species and to tease apart cryptically varying taxa (Hebert et al., 2003a). The most frequently used gene for this task is cytochrome *c* oxidase I (COI) from the mitochondrion. Forensic identifications—often of relevance to conservation—will undoubtedly be enhanced by COI sequencing, and any standardization of genetic methods and data has some inherent advantages. However, it should also be appreciated that basing forensic identifications on only one or a few genes has several potential pitfalls (Moritz & Cicero, 2004), and that ultimately much richer genomic characterizations will be desirable, especially in problematic situations.

Additional Topics

Evolutionary response to environmental changes (such as climate alterations, introductions of invasive species, and so on) is a primary theme of this current volume. Conservation genetics has close links to this topic, too, if for no other reason than that evolution is, by definition, genetic change across time. How will organisms and their genomes respond to current and near-future environmental challenges? The general answer is clear: They will respond exactly as populations have responded across the millennia—by adapting or

by going extinct. The only differences between current ecological changes (such as global warming and habitat fragmentation fueled by human actions) and those of bygone eras are, arguably, the faster pace of many current ecological shifts, and, less arguably, the global pervasiveness of the environmental alterations.

There are two empirical generalities from quantitative genetics that are relevant to conservation biology. The first is that most species have the genetic capacity to adapt rapidly to environmental challenges; the second is that the capacity for adaptation has limits. Similarly, two relevant empirical generalities from population genetics are that most species are spatially structured, but at the same time, populations are historically connected at various temporal depths. Two generalities from evolutionary genetics are that adaptive evolution is pervasive, but so, too, is genetic extinction. Two empirical generalities from phylogenetics are that biodiversity can be exuberant and tenacious but, paradoxically, that it can also be fragile. Thus, the overarching question for conservation biology is what balance, if any, will be achieved in the coming decades between each of these counterposing genetic forces? How many populations will adapt in place to the environmental challenges and how many will succumb? How many populations will shift their ranges to track the new environmental alterations and how many will have no migration corridors or other means of dispersal to find suitable habitats? In general, what fraction of populations and species will make it through this critical "bottleneck century?" These are the kinds of questions that will increasingly occupy the attention of conservation biologists.

CONCLUSIONS

My attempt to characterize conservation genetics based on the field's self-described literature has identified several major aspects of the discipline beyond its more traditional focus on inbreeding challenges in small populations. Many of these extensions were made possible by the fact that molecular markers have opened the entire biological world for genetic scrutiny at many levels in life's genealogical hierarchy, ranging from parentage and kinship in local populations to deep phylogeny in the Tree of Life. However, data from these new molecular technologies would have been of little use in conservation efforts or elsewhere had it not been

for the interpretive frameworks already provided (and since elaborated) by such time-honored fields as population and quantitative genetics, phylogenetics, and systematics. Defining the boundaries of conservation genetics will always be arbitrary to some extent because the field is intimately wedded to many of the other evolutionary and biodiversity disciplines.

Despite having compiled this overview, I do not wish to be interpreted as claiming any undue priority for genetic perspectives per se within the broader field of conservation biology. Genetic data and theory can be empirically and conceptually illuminating in many conservation efforts, but these endeavors are only a part of a larger mission. The truly pressing issue for the 21st century is the degree to which standing biodiversity, and the ecological and evolutionary processes that foster its maintenance, can be preserved at least quasi-intact for future generations. The ongoing biodiversity crisis is fundamentally a problem of environmental alteration and habitat loss caused by the collective weight of burgeoning human numbers. We have already destroyed a noticeable fraction of the planet's evolutionary genetic heritage. No genetic efforts, however valiant, can make more than a modest dent in solving the greater conservation problem—a challenge that will require full engagement of the life sciences as well as enlightened societal attitudes and steadfast political will.

SUGGESTIONS FOR FURTHER READING

Two edited volumes on molecular approaches to conservation genetics—one by Smith and Wayne and another by Avise and Hamrick—both appeared in 1996. An excellent authored textbook on conservation genetics is by Frankham and coworkers (2002), and a broader treatment of conservation biology is by Groom and colleagues (2005). Recommended source books that introduce various disciplines closely allied to conservation genetics are as follows: phylogeography (Avise, 2000), molecular phylogenetics and systematics (Hillis et al., 1996), molecular markers in ecology and evolution (Avise, 2004), inbreeding and outbreeding (Thornhill, 1993), and metapopulation biology (Hanski & Gilpin, 1997).

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