

OPINION

Preserving genes, species, or ecosystems? Healing the fractured foundations of conservation policy

BRIAN W. BOWEN

Department of Fisheries and Aquatic Sciences, University of Florida, 7922 NW 71st Street, Gainesville, FL 32653, USA

Abstract

The scientific foundations of conservation policy are the subject of a recent tripolar debate, with systematists arguing for the primacy of phylogenetic rankings, ecologists arguing for protection at the level of populations or ecosystems, and evolutionary biologists urging more attention for the factors that enhance adaptation and biodiversity. In the field of conservation genetics, this controversy is manifested in the diverse viewpoints of molecular systematists, population biologists, and evolutionary (and quantitative) geneticists. A resolution of these viewpoints is proposed here, based on the premise that preserving particular *objects* (genes, species, or ecosystems) is not the ultimate goal of conservation. In order to be successful, conservation efforts must preserve the *processes* of life. This task requires the identification and protection of diverse branches in the tree of life (phylogenetics), the maintenance of life-support systems for organisms (ecology), and the continued adaptation of organisms to changing environments (evolution). None of these objectives alone is sufficient to preserve the threads of life across time. Under this temporal perspective, molecular genetic technologies have applications in all three conservation agendas; DNA sequence comparisons serve the phylogenetic goals, population genetic markers serve the ecological goals, quantitative genetics and genome explorations serve the evolutionary goals.

Keywords: biodiversity, bioheritage, conservation genetics, temporal conservation

Received 11 February 1999; revision received 10 June 1999; accepted 13 July 1999

'The load of tomorrow, added to that of yesterday, carried today makes the strongest falter'
Sir William Osler, physician (1849–1919; quoted in Franklin 1951)

Introduction

Recent attempts to put conservation priorities on a scientific foundation have stalled over a tricotomy of opinions that correspond approximately to the biological disciplines of systematics, ecology, and evolution. Systematists argue that conservation efforts should be directed toward distinct taxa because these contribute to overall biodiversity on a scale proportional to their morphological or genetic distinctiveness. Ecologists maintain that landscapes and ecosystems should be the primary medium for conservation efforts because they provide the essential life-support system for endangered as well as

nonendangered taxa. Both systematic and ecological views have philosophical roots that extend back through human history (Meffe & Carroll 1997), but the debate between these schools has been particularly contentious in recent years (Franklin 1993; Forey *et al.* 1994; Wheeler & Cracraft 1996). A relatively new school of thought based on evolutionary theory has argued that conservation efforts should focus on preservation of the genetic diversity that allows biota to adapt to new conditions (see Frankel 1974; Lande & Shannon 1996; Lynch 1996). This concept can be extended to speciose groups that may be the source of future biodiversity (Erwin 1991).

Should conservation efforts be directed toward distinct taxa, ecosystems, or the progenitors of future biodiversity? These three perspectives appear to generate conflicting priorities for conservation efforts. The motivations for these systematic, ecological, and evolutionary agendas are quite different and may correlate to emerging subdisciplines under the umbrella of conservation biology. Four case histories are used to illustrate the motivations behind

Correspondence: B. W. Bowen. E-mail: bowen@gnv.ifas.ufl.edu

each agenda, and to suggest the possibility of a reconciliation among these three viewpoints. In essence, the unifying theme proposed here is that conserving biota requires three complementary steps: (i) identification of diverse organismal lineages (the systematic regime); (ii) protection of the life-support system for these lineages (the ecological regime); and (iii) maintenance of the conditions that generate new lineages (the evolutionary regime).

Molecular genetic methodologies can contribute to all three agendas, with techniques that resolve relationships from family pedigrees to Cambrian separations. When conservation genetics is considered under this tripolar framework, particular genetic techniques can be viewed as serving one of three conservation goals corresponding to systematics, ecology, or evolution.

Systematic perspective: the coelacanth

A prominent criterion for conservation is phylogenetic distinctiveness. Under this approach, highly distinct biota such as 'living fossils' contribute disproportionately to overall biodiversity, as reflected in taxonomic rank, and hence should receive a high conservation priority. One such living fossil is the coelacanth, a primitive bony fish thought to be extinct for 70 My prior to rediscovery in the 1930s (Smith 1939). *Latimeria chalumnae* is a benthic browser that occurs at low density in a few locations in the Indian Ocean (Fricke *et al.* 1991; Erdmann *et al.* 1998). Under the criteria for ecosystem health, the coelacanth might merit a low conservation priority. As a progenitor of future evolutionary radiations, this species is perhaps an unlikely candidate (but see below). Under the criteria of phylogenetic distinctiveness, the conservation of this animal is an extremely high priority.

The importance of defining taxonomic (or phylogenetic) units for conservation is well established (Wheeler & Cracraft 1996), but this approach is prone to accusations of anthropocentric bias. Several authors have argued that living fossils such as the coelacanth are curiosities, or charismatic megafauna, with no objective basis for preservation (see Erwin 1991). In counterargument, the extant coelacanth has provided a wealth of information on morphological and molecular evolution of vertebrates (Balon *et al.* 1988; Stock *et al.* 1991; Meyer & Dolven 1992). Similar to the ancient rocks sought by geologists to reveal the origins of our planet, important chapters in the history of life are etched in this organism, and much of this information can be found nowhere else.

The scientific value of the coelacanth is coupled with a historical value. The conservation of the coelacanth is not motivated by ecological role or future evolutionary potential, but by concern for the biological heritage (bioheritage) of this planet. As noted by Gould (1996), wise stewardship must include preservation of the links to

earlier phases of planetary history. While scientists and the public generally agree on the importance of preserving bioheritage, this perspective is still vulnerable to charges of anthropocentrism. Fortunately, objective standards are available that closely parallel human interest in ancient and morphologically distinct biota: the basis for preserving the coelacanth and other species can be expressed in terms of taxonomic rank and distinctiveness in morphological and genetic comparisons. In this regard, DNA sequence information provides a ubiquitous yardstick for measuring the uniqueness of taxa (Avice 1989).

Ecological perspective: the Florida panther

Habitat destruction is the single biggest factor in eroding biodiversity, and management schemes directed at particular species are doomed without consideration of habitat health (Lovejoy 1996). These and related considerations mandate an ecosystem approach to conservation, in which representative habitats, and those with high species richness, are earmarked for protection. An important premise of this approach is that the conservation of an ecosystem is not contingent on the presence of endangered species (Schmidt 1996), a key conceptual distinction between systematic and ecological approaches. Instead, species that play an essential role in ecological processes are recognized as high conservation priorities. For example, the re-establishment of large predators in North America is motivated, in part, by a desire to restore ecosystem functions.

Despite extraordinary efforts by state and federal agencies, the native panthers in southern Florida (*Puma concolor coryi*) now number less than 50 and continue to dwindle towards extinction. Decades of industrial-scale agriculture, coupled with an expanding human population, have reduced and degraded the habitat available to this feline predator. Under the criterion of taxonomic distinctiveness, the Florida panther may not merit a high priority because it is one of 30 recognized subspecies. Low genetic diversity and suspected inbreeding depression (Roelke *et al.* 1993) make this subspecies an unlikely candidate for generating future biodiversity. However, if the unique ecosystems of southern Florida are to be repaired, it is desirable to restore the role of top predator. The recognition of ecological role was a deciding factor in a recent decision to introduce Texas panthers (*P.c. stanleyana*) to supplement the dwindling native stock of Florida panthers. In this instructive case history, wildlife managers weighed the priorities of preserving a distinct phylogenetic lineage on the one hand, and maintaining a feline predator in south Florida on the other, and decided that the latter consideration carried greater weight. As one biologist expressed it, 'We can either have the Florida panther, or we can have panthers in Florida.' The consideration of these multiple priorities heralds a

new level of maturity in the implementation of conservation policy.

One problem with the ecology-based approach is that ecosystems are difficult to delineate, and estimates of the minimal size of nature reserves vary widely (Grumbine 1990). Another problem is that endangered taxa may not be perceived as high priorities if they have previously been reduced below the point where they serve ecosystem functions. The strength of the ecosystem approach lies in the pragmatic goals of perpetuating existing support systems for life. In practice, this approach requires information on the natural history, population structure, and interactions of coexisting species. Most conservation actions are undertaken at the level of ecosystems, and it is inevitable that these efforts consume the majority of resources available for conservation.

Evolutionary perspective: the African cichlid fishes

Population biologists have long recognized that genetic diversity allows species to respond to environmental challenges (Wright 1932; Soulé 1987; Lande & Shannon 1996). Based on this premise, genetic diversity is widely accepted as a foundation for future organismal diversity and corresponding conservation efforts are directed at preserving the existing genetic variation within endangered species (see Lynch 1996; Storfer 1996). These principles, applied in a taxonomic context, indicate that speciose groups (especially those with novel adaptations) may be the wellspring of future biodiversity (Erwin 1991). In contrast, living fossils may be the last vestiges of previous evolutionary flourishes, and thus not strong candidates for generating future biodiversity.

A prominent caveat in this line of reasoning is that biologists cannot predict which species will be the source of future evolutionary radiations (Bowen 1998). To accomplish this would solve a fundamental evolutionary paradigm: how do new species arise? Evolutionary biologists have made substantial progress in understanding the processes of speciation (Eldredge & Gould 1972; Carson & Templeton 1984; Otte & Endler 1989; Palumbi 1994; Veron 1995; Schluter 1996; Smith *et al.* 1997), but few would argue that the issue has been resolved. A second caveat is that speciose groups may include highly specialized taxa that are susceptible to extinction, and hence are evolutionary dead-ends (see Elliot 1986).

Accepting the limitations above, several criteria may nonetheless indicate future evolutionary potential, including rapid morphological differentiation and novel adaptations (the niche expansion criterion). The cichlid fishes of the African Great Lakes qualify in both categories. This group of over 400 species is characterized by extreme trophic and morphological diversification (Fryer & Iles

1972). In some cases, however, species are indistinguishable with molecular genetic assays (Moran & Kornfield 1993; Stauffer *et al.* 1995). Furthermore, the importance of any single species to ecosystem function may not be high. Hence, African cichlids may be a conservation priority in terms of evolutionary potential, but any single species may be a low priority in terms of phylogenetic distinctiveness and ecological role.

Even if scientists could accurately identify the well-springs of future evolutionary radiations, the criterion of evolutionary potential is clearly not sufficient by itself as a foundation for conservation priorities. Taken to one extreme, the philosophy of protecting speciose groups would mandate conservation efforts for bacteria. In practice, this conservation priority may be the least resource intensive. The progenitors of future biodiversity probably include groups that are abundant or widespread. In the absence of robust criteria to predict the biological successes of the future, the preservation of diverse ecosystems will probably include many of the organisms that qualify as conservation concerns in this category.

Intersection of conservation goals: the leatherback sea turtle

Conservation programmes can be viewed as serving one of three goals corresponding to the disciplines of systematics, ecology, and evolution. However, it is inevitable (and desirable) that these three conservation agendas will overlap, and that some populations, species, or ecosystems will qualify as priorities under more than one discipline. The leatherback sea turtle (*Dermochelys coriacea*) may qualify under all three criteria. It is distinguished at the taxonomic family level from other turtles and is highly divergent in DNA sequence comparisons (Bowen & Karl 1996; Dutton *et al.* 1996). As the sole representative of a lineage that traces back to the Jurassic period, this species clearly merits priority under the criteria of systematics and bioheritage. The leatherback turtle is also one of the few vertebrates that feeds on jellyfish (Scyphozoa), indicating a potentially important role in oceanic ecosystems. Finally, a suite of unique morphological and physiological adaptations allows this turtle to forage in the freezing waters of Labrador and the Gulf of Alaska. The leatherback turtle has transcended the barriers of being a reptile (Rhodin 1985) and therefore is a strong candidate for protection under the criterion of evolutionary potential. In summary, defensible arguments can be made to protect this endangered species on systematic, ecological, and evolutionary grounds.

A temporal framework for conservation biology

The conservation of distinct taxa such as the coelacanth is

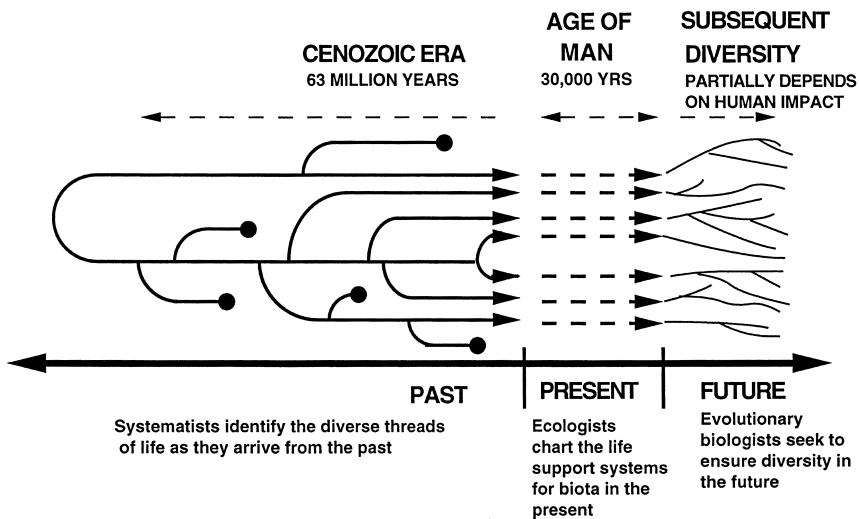


Fig. 1 The temporal framework for setting conservation priorities allocates responsibilities in three distinct temporal spheres (past, present, and future) to three disciplines (systematics, ecology, and evolution). The tree used here is based on the history of sea turtles inferred from molecular sequence comparisons (Bowen & Karl 1996; Dutton *et al.* 1996). The process of conserving sea turtles may start with the systematists identifying seven extant species which require protection. Subsequently, ecologists identify the key habitat features that allow sea turtles to survive and thrive on an ecological time-scale of a few tens of thousands of years. Finally, evolutionary biologists identify the raw materials for future prosperity and diversification.

motivated by the need to maintain the primary branches in the tree of life (the systematic perspective). These priorities are expressed in terms of morphological, genetic, or taxonomic differentiation: yardsticks based on evolutionary separations which have accumulated in the past. The conservation of ecosystems and key species such as feline predators is motivated by the desire to retain a vibrant biosphere, both for human prosperity and for the maintenance of extant biota (the ecological perspective). These priorities are based on ecosystem health, a perspective that is rooted in the present. The conservation of speciose groups such as the African cichlids is motivated by an appreciation for the processes that promote adaptation and speciation (the evolutionary perspective). These priorities are based on the production of new life forms in the future.

In the cases outlined above, conservation agendas based on systematics, ecology, or evolution generate very different priorities for individual taxa. Yet these need not be conflicting priorities, nor do they indicate faulty paradigms. When viewed in a temporal framework, these three agendas are strikingly complementary: the systematic focus on bioheritage (the past), the ecological focus on ecosystem integrity (the present), and the evolutionary focus on novel adaptations (the future). Considered in this light, these three perspectives reveal the temporal nature of conservation biology (Fig. 1).

The role of genetics in conservation

Conservation priorities can be classified under the three general headings of systematics, ecology, and evolution. Each of these disciplines draws on a different set of specialists, and each set of specialists carries a different toolbox. How are genetic studies relevant to the three domains of conservation? Prior to the advent of biochemical and molecular methodologies, it could be argued that genetic studies were primarily the domain of

the evolutionary biologists. However, four decades of technical advances have introduced genetic methodologies into the toolboxes of ecologists and systematists as well. Just as conservation efforts can be motivated by one (or more) of three agendas, the genetic technologies which serve these agendas can be quite distinct.

The introduction of genetics into systematics, and the corresponding fusion of molecular biology and organismal history has been famously successful as evidenced by numerous books including *Molecular Systematics* (Hillis *et al.* 1996) and journals such as *Molecular Phylogenetics and Evolution*. The essence of this field is comparisons of appropriate DNA sequences, which provide a universal template from which to make inferences about phylogenetic relationships. One of the most valuable contributions of molecular systematics to conservation is the identification of cryptic phylogenetic separations that are masked by conservative morphologies (Garcia *et al.* 1998; Clark *et al.* 1999; Roman *et al.* 1999; but see Karl & Bowen 1999). DNA sequence comparisons also allow the estimation of branch lengths on phylogenetic trees, something that is rarely possible with morphology-based systematics. These branch lengths are valuable in themselves to draw conclusions about the distinctiveness of taxa (Avice 1989). However, when coupled with estimates of mutation rate, branch lengths can be used to estimate the ages of separations. Molecular clock calibrations add an exciting new dimension to phylogenetic studies, and have clear utility for setting conservation priorities. As the value of systematic studies in conservation is widely accepted (Forey *et al.* 1994), so too is the utility of molecular phylogenetic studies.

The ultimate value of genetics in ecology is not a subject of universal agreement, but it is beyond dispute that genetic studies, when coupled with field studies, can yield powerful insights relevant to conservation. A primary goal of ecological genetics, as indicated by contributions to

the journal *Molecular Ecology*, is to resolve relationships from family pedigrees to intraspecific populations. With hypervariable nuclear loci, researchers can determine mate choice, reproductive behaviour, pedigrees, and social structure. These efforts require months in the laboratory, but produce information that could require years of field studies. Population genetic surveys of organellar and nuclear DNA are powerful tools for resolving wildlife management units (MUs: Moritz 1994) and the connectivity of proximate ecosystems (Joseph *et al.* 1995; Avise 1996; Schneider *et al.* 1998). All of this natural history information has applications in conservation.

The role of evolutionary genetics in conservation is still developing. After an initial phase embodied by the goal of preserving as much genetic diversity as possible, researchers have moved into a more sophisticated search for the genetic diversity that actually influences evolutionary processes and allows adaptation to changing conditions. Quantitative genetics seems to have an increasingly vital role (Storfer 1996). As noted by Lynch (1996), much of the genetic diversity observed in wild populations of plants and animals is probably irrelevant to evolutionary processes, and therefore irrelevant to the conservation of evolutionary processes. However, the general goal of preserving genetic diversity is undiminished.

Finally, a growing body of evidence indicates that mutations at developmental and regulatory operons are important evolutionary catalysts. Transposons can insert themselves at locations in the genome that will alter the expression of adjacent loci (McDonald 1990). Changes in protein structure via mutation can disrupt the recognition of gametes (Palumbi 1994; Swanson & Vacquier 1998). These and related classes of genomic changes probably enable the development of evolutionary novelty and new species (Krieger & Rose 1986). As the various 'genome' projects continue to unravel eukaryotic chromosomes, it is likely that the field of molecular evolution will take quantum steps in identifying the genetic elements that influence organismal evolution. These discoveries may, in turn, provide criteria for identifying geminate evolutionary lineages and for conserving the means of generating future biodiversity.

Summary

A recent controversy, apparent at the INTECOL symposium and other recent scientific exchanges, stems from a dispute over whether conservation priorities should be formulated in terms of ecology, phylogeny, or genetic diversity. In the field of conservation genetics, this controversy is embodied by the diverse viewpoints of population biologists, molecular systematists, and evolutionary biologists. The solution to this dispute begins with the recognition that preservation of any of these objects (genes, species

or ecosystems) alone is futile. Perpetuating species without ecosystems makes as much sense as preserving ecosystems without species. Perhaps the solution to this dispute includes the recognition that conservation is not about protecting objects, it is about protecting a process: life. Conservation is based on a mandate to maintain the threads of life as they arrive from the past, abide in the present, and depart for the future. Under the temporal perspective outlined above, the disciplines of systematics, ecology, and evolution each contribute uniquely and irreplaceably to conservation.

Acknowledgements

This essay was distilled from discussions or correspondence with J. C. Avise, R. M. Ball, A. L. Bass, L. C. Branch, D. E. Campton, J. Colborn, L. Farrell, S. A. Karl, R. C. Klinger, G. Meffe, P. E. Moler, C. Moritz, A. Muss, W. S. Nelson, S. J. O'Brien, A. Popadic, J. Roman, R. S. Waples, and M. Zacks. Their assistance does not connote their acquiescence. Special thanks to Stew Grant for review and discussions. Thanks to an anonymous reviewer for helpful comments, and to Tim King for encouragement. The author's research programme is supported by the U.S. National Science Foundation, National Marine Fisheries Service, and Fish and Wildlife Service.

References

- Avise JC (1989) A role for molecular genetics in the recognition and conservation of endangered species. *Trends in Ecology and Evolution*, **4**, 279–281.
- Avise JC (1996) Towards a regional conservation genetic perspective: Phylogeography of faunas in the southeastern United States. In: *Conservation Genetics; Case Histories from Nature* (eds Avise JC, Hamrick JL), pp. 431–470. Chapman & Hall, New York.
- Balon EK, Bruton MN, Fricke H (1988) A fiftieth anniversary reflection on the living coelacanth, *Latimeria chalumnae*: some new interpretations of its natural history and conservation status. *Environmental Biology of Fishes*, **23**, 241–280.
- Bowen BW (1998) What is wrong with ESUs? The gap between evolutionary theory and conservation principles. *Journal of Shellfish Research*, **17**, 1355–1358.
- Bowen BW, Karl SA (1996) Population genetics, phylogeography, and evolution. In: *The Biology of Sea Turtles* (eds Lutz PL, Musick JA), pp. 30–50. CRC Press, Boca Raton, Florida.
- Carson HL, Templeton AR (1984) Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annual Review of Ecology and Systematics*, **15**, 97–131.
- Clark AM, Bowen BW, Branch LC (1999) Effects of natural habitat fragmentation on an endemic lizard (*Sceloporus woodi*): an historical perspective based on an mtDNA gene genealogy. *Molecular Ecology*, **8**, 1093–1114.
- Dutton PH, Davis SK, Guerra T, Owens D (1996) Molecular phylogeny for marine turtles based on sequences of the ND4-leucine tRNA and control regions of mitochondrial DNA. *Molecular Phylogenetics and Evolution*, **5**, 511–518.
- Eldredge N, Gould SJ (1972) Punctuated equilibria: an alternative to phyletic gradualism. In: *Models in Paleobiology* (ed. Schopf TJM), pp. 82–115. Freeman, Cooper, San Francisco.
- Elliot DK (1986) *Dynamics of Extinction*. Wiley, New York.

- Erdmann MV, Caldwell RL, Moosa MK (1998) Indonesian 'King of the Sea' discovered. *Nature*, **395**, 355.
- Erwin TL (1991) An evolutionary basis for conservation strategies. *Science*, **253**, 750–752.
- Forey PL, Humphries CJ, Vane-Wright RI (1994) *Systematics and Conservation Evaluation*, Systematics Association Special Volume no. 50. Clarendon Press, Oxford.
- Frankel OH (1974) Genetic conservation: our evolutionary responsibility. *Genetics*, **78**, 53–65.
- Franklin AW (1951) *A way of Life, and Selected Writings of Sir William Osler*. Oxford Press, Cambridge.
- Franklin JF (1993) Preserving biodiversity: species, ecosystems, or landscapes. *Ecological Applications*, **3**, 202–205.
- Fricke HW, Hissmann K, Schauer J, Reinicke O, Kasang L, Plante R (1991) Habitat and population size of the living coelacanth *Latimeria chalumnae*. *Environmental Biology of Fishes*, **32**, 287–300.
- Fryer G, Iles T (1972) *The Cichlid Fishes of the Great Lakes of Africa*. Oliver and Boyd, London.
- García-Rodríguez AI, Bowen BW, Domning D *et al.* (1998) Phylogeography of the West Indian manatee (*Trichechus manatus*): how many populations and how many taxa? *Molecular Ecology*, **7**, 1137–1149.
- Gould SJ (1996) The dodo in the caucus race. *Natural History*, **105**, 22–33.
- Grumbine RE (1990) Protecting biological diversity through the greater ecosystem concept. *Natural Areas Journal*, **10**, 114–120.
- Hillis DM, Moritz C, Mable BK (1996) *Molecular Systematics*. 2nd edn. Sinauer Associates, Sunderland, Massachusetts.
- Joseph L, Moritz C, Hugall A (1995) Molecular support for vicariance as a source of diversity in rainforests. *Proceedings of the Royal Society of London B*, **260**, 177–182.
- Karl SA, Bowen BW (1999) Evolutionary significant units versus geopolitical taxonomy: molecular systematics of an endangered sea turtle (genus *Chelonia*). *Conservation Biology*, **13**, 990–999.
- Kriebler M, Rose MR (1986) Molecular aspects of the species barrier. *Annual Review of Ecology and Systematics*, **17**, 465–485.
- Lande R, Shannon S (1996) The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution*, **50**, 434–437.
- Lovejoy TE (1996) Biodiversity: what is it? In: *Biodiversity II* (eds Reaka-Kudla ML, Wilson DE, Wilson EO), pp. 7–14. Joseph Henry Press, Washington, DC.
- Lynch M (1996) A quantitative-genetic perspective on conservation issues. In: *Conservation Genetics; Case Histories from Nature* (eds Avise JC, Hamrick JL), pp. 471–501. Chapman & Hall, New York.
- McDonald JF (1990) Macroevolution and retroviral elements. *Bioscience*, **40**, 183–191.
- Meffe GK, Carroll CR (1997) What is conservation biology? In: *Principles of Conservation Biology*, 2nd edn (eds Meffe GK, Carroll CR), pp. 3–28, Sinauer Associates, Sunderland, Massachusetts.
- Meyer A, Dolven SI (1992) Molecules, fossils, and the origin of tetrapods. *Journal of Molecular Evolution*, **35**, 102–113.
- Moran P, Kornfield I (1993) Retention of an ancestral polymorphism in the mbuna species flock (Pisces: Cichlidae) of Lake Malawi. *Molecular Biology and Evolution*, **10**, 1015–1029.
- Moritz C (1994) Defining 'evolutionary significant units' for conservation. *Trends in Ecology and Evolution*, **9**, 373–375.
- Otte D, Endler JA (1989) *Speciation and its Consequences*. Sinauer Associates, Sunderland, MA.
- Palumbi SR (1994) Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics*, **25**, 547–572.
- Rhodin AGJ (1985) Comparative chondro-osseous development and growth of marine turtles. *Copeia*, **1985**, 752–771.
- Roelke ME, Martenson JS, O'Brien SJ (1993) The consequences of demographic reduction and genetic depletion in the endangered Florida panther. *Current Biology*, **3**, 340–350.
- Roman J, Santhuff S, Moler P, Bowen BW (1999) Cryptic evolution and population structure of the alligator snapping turtle, *Macrolemys temminckii*. *Conservation Biology*, **13**, 135–142.
- Schluter D (1996) Ecological speciation of postglacial fishes. *Philosophical Transactions of the Royal Society of London B*, **351**, 807–814.
- Schneider CJ, Cunningham M, Moritz C (1998) Comparative phylogeography and the history of endemic vertebrates in the wet tropics rainforests of Australia. *Molecular Ecology*, **7**, 487–498.
- Schmidt K (1996) Rare habitats vie for protection. *Science*, **274**, 916–918.
- Smith JLB (1939) A living coelacanthid fish from South Africa. *Nature*, **143**, 748–750.
- Smith TB, Wayne RK, Girman DJ, Bruford MW (1997) A role for ecotones in generating rainforest biodiversity. *Science*, **276**, 1855–1857.
- Soulé ME (1987) *Viable Populations for Conservation*. Cambridge University Press, Cambridge, UK.
- Stauffer JR Jr, Bowers NJ, McKaye KR, Kocher TD (1995) Evolutionary significant units among cichlid fishes: the role of behavioral studies. In: *Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation* (ed. Nielsen JL), pp. 227–244. American Fisheries Society Symposium 17, American Fisheries Society, Bethesda, MD.
- Stock DW, Moberg KD, Maxson LR, Whitt GS (1991) A phylogenetic analysis of the 18S ribosomal RNA sequence of the coelacanth *Latimeria chalumnae*. *Environmental Biology of Fishes*, **32**, 99–117.
- Storfer A (1996) Quantitative genetics: a promising approach for the assessment of genetic diversity in endangered species. *Trends in Ecology and Evolution*, **11**, 343–348.
- Swanson WJ, Vacquier VD (1998) Concerted evolution in an egg receptor for a rapidly evolving abalone sperm protein. *Science*, **281**, 710–712.
- Veron JEN (1995) *Corals in Space and Time; the Biogeography and Evolution of the Scleractinia*. Comstock/Cornell, Ithaca, New York.
- Wheeler QD, Cracraft J (1996) Taxonomic preparedness: are we ready to meet the biodiversity challenge? In: *Biodiversity II* (eds Reaka-Kudla ML, Wilson DE, Wilson EO), pp. 435–446. Joseph Henry Press, Washington, DC.
- Wright S (1932) The role of mutation, inbreeding, cross-breeding, and selection in evolution. *Proceedings of the 6th International Congress of Genetics*, **1**, 356–366.

The author was originally inspired to seek a career in biology by a school of striped bass in Cape Cod Bay, a rogue humpback whale viewed from a small boat, and an inability to focus on more practical matters. The author is an assistant professor at University of Florida, and received training in biology at Providence College, marine biology at Virginia Institute of Marine Science, and genetics at University of Georgia. Current research interests include marine biogeography and the conservation genetics of aquatic organisms.
