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A Proposal to Eliminate Redundant Terminology for Intra-Species Groups

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Abstract

Many new terms have come into use for intra-species groups of animals defined with genetic criteria including subspecies, evolutionarily significant units, evolutionary units, management units, metapopulations, distinct population segments, populations, and subpopulations. These terms have redundant meanings and can lead to confusion for biologists, managers, and policy makers. I propose that for wildlife management we can simplify intra-species terminology and use only the terms subspecies, populations, and subpopulations. These 3 terms have roots in evolutionary and population biology and can incorporate genetic, demographic, and geographic considerations. (WILDLIFE SOCIETY BULLETIN 34(1):237–241; 2006)

Key words

intra-species, Endangered Species Act, population, redundant terminology, subpopulation, subspecies.

Recently, there has been a proliferation of terms used to describe groups of animals below the species level. For example, Wells and Richmond (1995) identified >30 terms used to describe groups generally referring to populations. They also discussed the problems with scientific communication associated with such extensive and redundant terminology. The importance of intra-species definitions is exemplified by the United States Endangered Species Act (ESA). The ESA allows listing of species, but it also allows listing of subspecies and distinct population segments (DPS) without clear definition of these terms. The importance of these intra-specific categories is evident in the large number of subspecies and DPS listed under the ESA. For example, more than 70% (57 of 81 listed taxa) of the listed mammals in the United States are identified as subspecies or DPS (http://endangered.fws.gov/wildlife.html). Examples of subspecies listed under the ESA with questionable subspecies status include the California gnatcatcher (*Polioptila californica californica*, Cronin 1997, Zink et al. 2000) and Preble's meadow jumping mouse (*Zapus hudsonius preblei*, Ramey et al. 2005). Other examples of indefinite subspecies designations that affect management and policy are given by Cronin (1993) and Zink (2004). The importance of clear definition of DPS has been recognized by the agencies administering the ESA (i.e., The United States Fish and Wildlife Service and National Marine Fisheries Service). These agencies noted: "Federal agencies charged with carrying out the provisions of the ESA have struggled for over a decade to develop a consistent approach for interpreting the term 'distinct population segment'" (Waples 1991:v); and ". . .it is important that the term 'distinct population segment' be interpreted in a clear and consistent fashion." (Federal Register 7 Feb. 1996, Vol 61:4722). The National Research Council (NRC 1995:55) recognized the importance of identification of intra-specific units for ESA consideration and stated: "Unless we agree to preserve all endangered or threatened organisms of all taxonomic ranks, we must find ways to identify those groups of organisms we consider to be significant."

Genetics is increasingly being used to designate intra-specific groups, including subspecies, DPS, evolutionarily significant units (ESU), evolutionary units (EU), management units (MU), metapopulations, populations, and subpopulations (Moritz 1994, Moritz et al. 1995, NRC 1995, Avise 2000). These groups are partially or entirely defined by genetic similarity, often inferred from molecular genetic data. Genetic similarity is assumed to reflect recent common ancestry of, or extant gene flow among, groups of animals. Groups thus identified are frequently designated as a unit for management or conservation.

In a previous paper, I discussed the utility and limitations of genetic data in wildlife management, including identification of units for management and conservation (Cronin 1993). I thought it would be useful to revisit this issue because of the introduction of new terms defined with genetic considerations. My objective in this paper is to review several intra-species terms defined with genetics (subspecies, ESU, EU, MU, metapopulation, DPS, population, subpopulation) and propose a way to simplify their use.

Intra-Species Groups

Before discussing intra-species groups, it is useful to define a species. The most common species concept is that of biological species, identified with a Latin binomial name (e.g., *Odocoileus virginianus,* white-tailed deer). Biological species are groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr 1963). Other species concepts are potentially useful (e.g., phylogenetic species, genetic species, Avise 1994, 2000, NRC 1995, Baker et al. 2003), but they are beyond the scope of this discussion. Identification of species with any of these concepts is not always definitive because of uncertainties about reproductive compatibility in natural populations, morphologically similar sibling species, and unknown phylogenetic relationships. However for most wildlife management applications, identification of species is not a problem compared to identification of intra-species groups.

It is also important to recognize there are intraspecific groups identified without regard for genetic ancestry. For example, ecotypes are con-specific groups with similar ecological adaptations regardless of geneological relationship. Such groups are discussed elsewhere (e.g., Wells and Richmond 1995, Courtois et al. 2003, Cronin et al. 2005).

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Subspecies

A subspecies has been defined as a geographically defined group of local populations which differ from other such groups (Mayr 1969, Dobzhansky 1970). Subspecies are given a Latin trinomial name in taxonomic classification (e.g., *Odocoileus hemionus hemionus,* Rocky Mountain mule deer; *O. h. sitkensis,* Sitka black-tailed deer). However, the subspecies concept has been criticized by several authors (Wilson and Brown 1953, Ryder 1986, Cronin 1997, Ehrlich 2000, Zink 2004). Wilson and Brown (1953) contended that the subspecies concept is so arbitrary a concept that it should be abandoned. Vanzolini (1992:189) noted that "… present applications of the subspecies concept are uneven, frequently undocumented, and lead to no improvement of either evolutionary theory or practical taxonomy." Futuyma (1986) noted that there is so much variation among populations of most species that some combination of characters will distinguish each population from others and, consequently, there is no clear limit to the number of subspecies that can be recognized. Ehrlich (2000:49) echoed this sentiment: "Widespread species thus can be divided into any number of different sets of 'subspecies' simply by selecting different characteristics on which to base them," and he summarized the issue: "As is the case with other species, geographic variation in human beings does not allow *Homo sapiens* to be divided into natural evolutionary units. That basic point…has subsequently been demonstrated in a variety of organisms…and use of the subspecies (or race) concept has essentially disappeared from the mainstream evolutionary literature" (Ehrlich 2000:291). These problems associated with subspecies are manifested in the lack of concordance of patterns of molecular genetic variation and subspecies boundaries for several wildlife species (Cronin 1993, Zink 2004). This includes such high-profile groups as grizzly bears (*Ursus arctos*, Talbot and Shields 1996; Paetkau et al. 1998; Waits et al. 1998) and spotted owls (*Strix occidentalis*, Haig et al. 2001). Zink (2004) notes that more than 90% of the avian subspecies in continental North America (i.e., not on islands) do not qualify as subspecies if rigorous tests for congruence of characters are applied.

Despite these negative aspects of the subspecies category, biologists should recognize that there is important geographic variation within species. Wilson (1994) notes that his early rejection of subspecies (Wilson and Brown 1953) overstated the case because some populations can be defined with genetic traits that vary over geography in a concordant manner. Other authors have also recently noted the potential utility of subspecies. For example, Avise and Ball (1990:59–60) proposed that "Subspecies are groups of actually or potentially interbreeding populations, phylogenetically distinguishable from, but reproductively compatible with, other such groups. Importantly, the evidence for phylogenetic distinction must normally come from the concordant distributions of multiple, independent, genetically based traits." This gives a potentially useful framework for designation of subspecies.

In summary, the subspecies has been a loosely applied concept, with little objective rigor. However, the concept has utility in recognizing potentially important geographic variation and may be applied with proper application of taxonomic principles. Because subspecies can be listed under the ESA and are the basis of some trophy hunting classifications, they are important from a management standpoint, but many existing designations of subspecies are in need of revision with phylogenetic analyses. Geist et al. (2000) provide an insightful discussion of these concepts and the current subspecies status of several wildlife species.

Evolutionarily Significant Units and Evolutionary Units

The term Evolutionarily Significant Unit (ESU) originally was suggested by zoo biologists as a potential substitute for the subspecies category in conservation efforts (Ryder 1986). However, the concept has taken on 2 definitions in the literature and relies on somewhat arbitrary criteria (Avise 2000, Milius 2000, DeWeerdt et al. 2002).

One definition of an ESU is a group with monophyletic mitochondrial DNA (mtDNA) and significant allele frequency differences at nuclear loci compared to other groups (Moritz 1994, Moritz et al. 1995). Other authors also recommend the use of a phylogenetic approach for identification of ESUs (Bernatchez 1995, Mayden and Wood 1995). Evolutionarily Significant Units defined by monophyletic mtDNA essentially conform to the recent subspecies definition as described above (Avise and Ball 1990). MtDNA phylogeny is described elsewhere (e.g., Cronin 1993; Avise 1994, 2000), but basically it refers to the geneological relationships of mtDNA genotypes as inferred from DNA sequence analysis. Genotypes with similar DNA sequences are considered as sharing a more recent common ancestral genotype than divergent genotypes. It is important to recognize that this approach has potential flaws because mtDNA phylogeny (which represents a single gene phylogeny) may not reflect the overall differentiation of species or populations (Pamillo and Nei 1988, Cronin 1993).

This important point was recognized by Pääbo (2000), who questioned the designation of grizzly bear ESUs based on the phylogeny of mtDNA control region and cytochrome *b* sequences (Waits et al. 1998; Leonard et al. 2000). Pääbo's basic question is how much mtDNA differentiation is meaningful? In this case estimates of the overall sequence divergence of the mtDNA genotypes that define the proposed grizzly bear ESUs in different geographic areas is about 1–3% (Cronin et al. 1991). However, mtDNA genotypes of black bears (*Ursus americanus*) within geographic locations in Montana and Oregon have twice as much (5%) sequence divergence (Cronin et al. 1991). In this case, the divergence of mtDNA genotypes within a group of black bears is larger than that between the grizzly bear groups proposed for ESU status. The use of mtDNA sequence variation can provide useful information, but its meaning in terms of population differentiation is open to interpretation.

A second definition of ESU has been applied to Pacific salmon and steelhead (*Oncoryhnchus* spp.) by the National Marine Fisheries Service (NMFS). In this case an ESU is a population (or a group of populations) that is substantially reproductively isolated from con-specific population units, and represents an important component in the evolutionary legacy of the species (Waples 1991, 1995). Such ESUs are considered distinct population segments (DPS) under the ESA. Substantial reproductive isolation refers to limited gene flow between ESUs, often measured with molecular genetic markers. An important component of the evolutionary legacy of the species refers to various traits such as morphology, life history, and geographic distribution. This definition of ESU differs from that of Moritz (1994) and Moritz et al. (1995) primarily because substantial reproductive isolation, not mtDNA phylogeny, is used to differentiate groups.

There are obvious problems with the NMFS definition of ESU. First, note in the definition that an ESU is a population or group of populations, so it is a redundant term. Second, the term has an inherent value judgement (evolutionary significance) and reliance on arbitrary criteria. Neither the degree of reproductive isolation (substantial) nor the evolutionary significance (importance to the evolutionary legacy of the species) of populations is quantitatively defined. The indefinite nature of the term "evolutionarily significant" is one of the reasons why the National Research Council coined the term Evolutionary Unit (EU), without the word "significant" (NRC 1995). Third, ESU appears to be an exclusive term, and some populations will warrant this status; some will not. However, in the case of Pacific salmonids (chinook salmon *Oncorhynchus tshawytscha*, Myers et al. 1998; coho salmon *O. kisutch*, Weitkamp et al. 1995; steelhead, anadromous *O. mykiss*, Busby et al. 1996), all wild fish are in one ESU or another. Except for hatchery fish, there are no nonevolutionarily significant units. One could ask, if every group is evolutionarily significant, then why have the term? The term ESU was instituted to avoid the subjective and arbitrary designations of many subspecies (Ryder 1986), but has itself become subjective and arbitrary.

The NRC (1995) used the term "evolutionary unit" (EU) for identification of groups suitable for ESA listing. An EU is a group of organisms that represents a segment of biological diversity that shares evolutionary lineage and contains the potential for a unique evolutionary future. EUs may differ in morphology, behavior, physiology, biochemistry, genetics, and geography. Genetic distinctiveness is considered a key characteristic of an EU. There are only subtle differences between the EU and ESU concepts and the NRC (1995) acknowledges that use of either will lead to similar results, especially for vertebrates.

Populations, Subpopulations, Distinct Population Segments, and Metapopulations

Population is perhaps the most general and widely used term for intra-species groups (Wells and Richmond 1995), and entire fields of study employ this term (e.g., population biology, population genetics). Populations of fish, marine mammals, and other aquatic animals often are referred to as stocks and the reader may consider this term synonymous with population for this discussion. At the highest level, the entire species can be considered an inclusive population (Dobzhansky 1970). At the middle level, a population can be considered as a group of component local populations or subpopulations. At the lowest level, a population is a group of individuals of a species in one geographic location (Mayr 1963). The terms deme, subpopulation, or local population are synonymous with this meaning.

The term metapopulation has recently come into use. Metapopulations are assemblages of local populations with migration (i.e., gene flow) among them (Hanski and Gilpin 1997). A metapopulation comprised of component populations, may be considered synonymous with a population comprised of component subpopulations (Lande and Barrowclough 1987, Hanski and Simberloff 1997, Futuyma 1986). Like the term ESU, the term metapopulation is redundant.

Another term with considerable importance in wildlife management is distinct population segment (DPS), which are units that can be listed under the ESA. As noted above, the NMFS designation of ESU is equivalent to a DPS for Pacific salmon and steelhead. Other groups, including fish, birds, and mammals, have been designated DPS for ESA purposes (http://endangered.fws.gov/wildlife.html). The criteria for designating a DPS include "...discreteness of the population segment in relation to the remainder of the species to which it belongs." (Federal Register 7 Feb. 1996, Vol 61:4725). A population may be considered discrete if it is "markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may provide evidence of this separation." (Federal Register 7 Feb. 1996, Vol 61 4725). Thus, genetic differentiation is one of the criteria considered in designating a DPS, and the term could be considered synonymous with population or subpopulation.

Management Units

The term management unit (MU) has recently been defined with genetic criteria. An MU is a demographically independent population or set of populations identified by differences in frequencies of mtDNA haplotypes or nuclear alleles, regardless of allele phylogeny (Moritz 1994; Moritz et al. 1995). Basically, an MU is a group with limited gene flow with other groups. In this genetic context, an MU can be considered synonymous with a subpopulation, local population, or DPS. Of course, the term management unit can be used in a completely nongenetic context, and management units frequently are based simply on geography, demography, or other factors (Cronin 1993, 1997, 2003, Avise 1995, Taylor and Dizon 1996).

An MU differs from the ESU of Moritz (1994) because the MU does not consider DNA-based allele phylogeny whereas the ESU does. Note however, that Moritz' MU conforms to the NMFS definition of ESU, as groups with limited gene flow (i.e., as indicated by different allele frequencies). That is, an MU by Moritz' criteria is essentially an ESU by NMFS' criteria. Recall that the ESU of NMFS is considered a DPS under the ESA, so presumably an MU can be a DPS.

A Proposal to Simplify Terms for Intra-Species Groups

It is clear from the preceding discussion and previous work (Wells and Richmond 1995), that the use of intra-species terms is inconsistent, redundant, and confusing. The terms ESU, EU, MU, and metapopulation resulted largely from genetics considerations (Waples 1991, 1995, Moritz 1994, Moritz et al. 1995, Hanski and Simberloff 1997). The term DPS resulted from a regulatory phrase (Federal Register 7 Feb. 1996, 61 FR 4722). The terms subspecies, population, and subpopulation are from pioneering research, thought, and syntheses on variation in natural populations (Mayr 1963, 1969; Dobzhansky 1970, Wright 1978).

In summary, aside from details that are largely irrelevant to wildlife management, it is reasonable to conclude that:

Subspecies = ESU (Mortiz 1994, definition) or EU;
Population = ESU (NMFS definition), subpopulation, EU, MU, or DPS;
Subpopulation = local population, deme, ESU (NMFS definition), EU, MU, or DPS.
Population composed of subpopulations = metapopulation composed of populations.

I propose that this redundancy can be eliminated if we restrict our use of intra-species terms to subspecies, population, and subpopulation. I would defer to those working with fish, marine mammals, and other aquatic animals if they prefer the terms stock and substock in lieu of population and subpopulation. The terms ESU, EU, MU, DPS, and metapopulation are not necessary for wildlife management.

This proposal will make a simpler system of intra-species terminology. If we apply the taxonomic practice of using the first terms applied to a taxon, the terms subspecies, population, and subpopulation have priority (i.e., their use preceded the others). In addition, this scheme is consistent in using the same prefix (sub) for divisions of a higher category (i.e., species-subspecies, population-subpopulation).

My proposal is not intended to ignore the contribution of genetics to wildlife management, but to simplify the use of terms. The use of the terms subspecies, population, and subpopulation allow consideration of genetics, in addition to demography and geography. For example, the widely used measure of population genetic subdivision, F_{st}, (Wright 1978) reflects differentiation of allele frequencies among subpopulations comprising a population (i.e., the "s" in F_{st} represents the term "subpopulation").

I recognize that there will be some problems with use of the terms I propose. For example, subspecies will remain vague because of old designations of groups for which there is limited phylogenetic information (Geist et al. 2000). Also, the terms population and subpopulation will be used interchangeably depending on the situation. However, my proposal is to simplify the use of terms rather than invent new terms for each situation. Descriptions can be added to the basic terms to fit specific cases.

Some examples will illustrate implementation of my proposal. We can say the black-tailed deer subspecies (*Odocoileus hemionus columbianus*, *O. h. sitkensis*) and mule deer subspecies (*O. h. hemionus*) differ morphologically, have phylogenetically distinct mtDNA, different nuclear allele frequencies, and include both clinal variation and hybrid contact zones (Carr et al. 1986, Cronin et al. 1988, Cronin 1991). This allows use of the subspecies concept, and gives specific descriptions of the groups. Instead of designating salmon ESUs, we can say that the population of chinook salmon in the Columbia River is composed of several subpopulations with different allele frequencies, run timing, and other life history traits. Another example is the Steller sea lion (*Eumetopias jubatus*), in which two DPS (western and eastern) have been identified in the Pacific Ocean and listed under the ESA. These groups have different mtDNA genotype frequencies, but nuclear microsatellite DNA allele frequencies are not different (Trujillo et al. 2004). One could say there is a Pacific Ocean population (or stock if you prefer) of Steller sea lions consisting of eastern and western subpopulations (or substocks). Another example with relevance to the ESA is the DPS of the California bighorn sheep (*Ovis canadensis californiana*) in the Sierra Nevada Mountains. In the Final Rule to list under the ESA the DPS was repeatedly referred to as a population composed of five subpopulations (Federal Register 65: 20–30, 3 January 2000).

It also is important to recognize that the terms population and subpopulation will be used at different geographic scales. For example, we can refer to the North American population, and Alaska subpopulation, of grizzly bears. Or we can refer to the Alaska population, and Kodiak Island subpopulation, of grizzly bears. Or we can refer to the Kodiak Island population, and local subpopulations in different parts of the island, of grizzly bears. The primary point is that there is no need to invoke the terms ESU, EU, MU, metapopulation, or DPS; we simply add precise descriptions to the basic terms subspecies, population, and subpopulation.

Ironically, the proliferation of terms created to describe intra-specific variation mimics the pre-evolutionary "typological thinking" in which variable groups (e.g., species, subspecies) were sorted into rigid classes. Darwin and the evolutionary synthesis of the 1900s instituted "population thinking," in which it is recognized that organisms occur in variable populations, not constant types (Mayr 2001). Now we have developed a confusing array of classes (i.e. terms) to describe what are basically populations. I see nothing to be gained from forcing groups of animals into an increasing array of redundant classes. I believe that use of simple terms, with appropriate descriptions of the variation within and between them, is the best way to maintain population thinking in the application of science in wildlife management.

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Literature Cited

Avise, J. C. 1994. Molecular markers, natural history, and evolution. Chapman and Hall, New York, New York, USA.

Avise, J. C. 1995. Mitochondrial DNA polymorphism and a connection between genetics and demography of relevance to conservation. Conservation Biology 9:686–690.

Avise, J. C. 2000. Phylogeography, the history and formation of species. Harvard University Press, Cambridge, Massachusetts, USA.

Avise, J. C., and R. M. Ball, Jr. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Oxford Survey of Evolutionary Biology 7:45–67.

Baker, R. J., M. B. O'Neill, and L. R. McAliley. 2003. A new species of desert shrew, *Notiosorex*, based on nuclear and mitochondrial sequence data. Occasional Papers, Museum of Texas Tech University Number 222:1–12.

Bernatchez, L. 1995. A role for molecular systematics in defining evolutionarily significant units in fishes. Pages 114–132 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland, USA.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon, and California. United States Department of Commerce/National Oceanic and Atmospheric Administration/National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Technical Memorandum NMFS-NWFSC-27. Seattle Washington, and Long Beach, California , USA.

Carr, S. M., W. Ballinger, J. N. Derr, L. H. Blankenship, and J. W. Bickham. 1986. Mitochondrial DNA analysis of hybridization between sympatric white-

tailed deer and mule deer in west Texas. Proceedings of the National Academy of Science USA 83:9576–9580.
Courtois, R., L. Bernatchez, J. P. Ouellet, and L. Breton. 2003. Significance of caribou (*Rangifer tarandus*) ecotypes from a molecular genetics viewpoint. Conservation Genetics 4:393–404.
Cronin, M. A. 1991. Mitochondrial and nuclear genetic relationships of deer (*Odocoileus* spp) in western North America. Canadian Journal of Zoology 69: 1270–1279.
Cronin, M. A. 1993. Mitochondrial DNA in wildlife taxonomy and conservation biology: cautionary notes. Wildlife Society Bulletin 21:339–348.
Cronin, M. A. 1997. Systematics, taxonomy and the Endangered Species Act: the example of the California gnatcatcher (*Polioptila californica*). Wildlife Society Bulletin 25:661–666.
Cronin, M. A. 2003. Research on deer taxonomy and its relevance to management. Ecoscience 10:333–343.
Cronin, M. A., S. C. Amstrup, G. W. Garner, and E. R. Vyse. 1991. Interspecific and intraspecific mitochondrial DNA variation in North American bears (*Ursus*). Canadian Journal of Zoology 69:2985–2992.
Cronin, M. A., M. D. MacNeil, and J. C. Patton. 2005. Variation in mitochondrial DNA and microsatellite DNA in caribou (*Rangifer tarandus*) in North America. Journal of Mammalogy 86:495–505.
Cronin, M. A., E. R. Vyse, and D. G. Cameron. 1988. Genetic relationships between mule deer and white-tailed deer in Montana. Journal of Wildlife Management 52:320–328.
DeWeerdt, S., K. Crandall, C. Moritz, E. Sinclair, R. Waples, R. Wayne, and A. Clark. 2002. What really is an Evolutionarily Significant Unit? Conservation Biology in Practice 3:1–17.
Dobzhansky, T. 1970. Genetics of the evolutionary process. Columbia University Press, New York, New York, USA.
Ehrlich, P. R. 2000. Human natures. Island Press, Washington, D.C., USA.
Futuyma, D. J. 1986. Evolutionary biology. Sinauer Associates, Sunderland, Massachusetts, USA.
Geist, V., B. O'Gara, and R. S. Hoffmann. 2000. Taxonomy and the conservation of biodiversity. Pages 1–26 *in* S. Demarais, and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice-Hall Upper Saddle River, New Jersey, USA.
Haig, S. M., R. S. Wagner, E. D. Forsman, and T. D. Mullins. 2001. Geographic variation and genetic structure in spotted owls. Conservation Genetics 2:25–40.
Hanksi, I. A., and M. E. Gilpin. 1997. Metapopulation biology, ecology, genetics, and evolution. Academic Press, San Diego, California, USA.
Hanski, I. A., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 *in* I. A. Hanksi, and M. E. Gilpin, editors. Metapopulation biology, ecology, genetics, and evolution. Academic Press, San Diego, California, USA.
Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87–123 *in* M. E. Soule, editor. Viable populations for conservation. Cambridge University Press, Cambridge, United Kingdom.
Leonard, J. A., R. K. Wayne, and L. Cooper. 2000. Population genetics of ice age brown bears. Proceedings of the National Academy of Science USA 97: 1651–1654.
Mayden, R. L., and R. M. Wood. 1995. Systematics, species concepts, and the evolutionarily significant unit in biodiversity and conservation biology. Pages 58–113 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland, USA.
Mayr, E. 1963. Populations, species, and evolution. Belknap Press, Harvard University Press, Cambridge, Massachusetts, USA.
Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill, New York, New York, USA.
Mayr, E. 2001. What evolution is. Basic Books, New York, New York, USA.
Milius, S. 2000. A fracas over a biological term could have huge consequences for conservation. Science News 158:250–252.
Moritz, C. 1994. Applications of mitochondrial DNA analysis in conservation: a critical review. Molecular Ecology 3:401–411.
Moritz, C., S. Lavery, and R. Slade. 1995. Using allele frequency and phylogeny to define units for conservation and management. Pages 249–262 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland, USA.
Myers, J. M., R. G. Kope, G. J. Bryant, D. Teel, L. J. Lierheimer, T. C. Wainwright, W. S. Grant, F. W. Waknitz, K. Neely, S. T. Lindley, and R. S. Waples. 1998. Status review of chinook salmon from Washington, Idaho, Oregon, and California. United States Department of Commerce. National Oceanic and Atmospheric Administration, Technical Memorandum NMFS-NWFSC-35, Seattle, Washington, Long Beach, California, Newport, Oregon, and Tiburon, California, USA.
National Research Council. 1995. Science and the Endangered Species Act. National Research Council, Committee on Scientific Issues in the Endangered Species Act. National Academy Press, Washington, D.C., USA.
Pääbo, S. 2000. Of bears, conservation genetics, and the value of time travel. Proceedings of the National Academy of Science USA 97:1320–1321.
Paetkau, D., G. Shields, and C. Strobeck. 1998. Gene flow between insular, coastal, and interior populations of brown bears in Alaska. Molecular Ecology 7:1283–1292.
Pamillo, P., and M. Nei. 1988. Relationships between gene trees and species trees. Molecular Biology and Evolution 5:568–583.
Ramey, R. R., H. P. Liu, C. W. Epps, L. M. Carpenter, and J. D. Wehausen. 2005. Genetic relatedness of the Preble's meadow jumping mouse (*Zapus hudsonius preblei*) to nearby subspecies of *Z. hudsonius* as inferred from variation in cranial morphology, mitochondrial DNA and microsatellite DNA: implications for taxonomy and conservation. Animal Conservation. 8:329–346.
Ryder, O. A. 1986. Species conservation and systematics: the dilemma of subspecies. Trends in Ecology and Evolution 1:1.
Talbot, S. L., and G. F. Shields. 1996. Phylogeography of brown bears (*Ursus arctos*) of Alaska and paraphyly within the Ursidae. Molecular Phylogenetics and Evolution 5:477–494.
Taylor, B. L., and A. E. Dizon. 1996. The need to estimate power to link genetics and demography for conservation. Conservation Biology 10:661–664.
Trujillo, R. G., T. R. Loughlin, N. J. Gemmel, J. C. Patton, and J. W. Bickham. 2004. Variation in microsatellites and mtDNA across the range of the Steller sea lion, *Eumetopias jubatus*. Journal of Mammalogy 85:338–346.
Vanzolini, P. E. 1992. Third world museums and biodiversity. Pages 185–198 *in* N. Eldredge, editor. Systematics, ecology, and the biodiversity crisis. Columbia University Press, New York, New York, USA.
Waits, L. P., S. L. Talbot, R. H. Ward, and G. F. Shields. 1998. Mitochondrial DNA phylogeography of the North American brown bear and implications for conservation. Conservation Biology 12:408–417.
Waples, R. S. 1991. Definition of "species" under the Endangered Species Act: application to Pacific salmon. United States National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Technical memorandum NMFS F/NWC-194, Seattle, Washington, USA.
Waples, R. S. 1995. Evolutionarily Significant Units and the conservation of biological diversity under the Endangered Species Act. Pages 8–27 *in* J. L. Neilsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland, USA.
Weitkamp, L. A., T. C. Wainwright, G. J. Bryant, G. B. Milner, D. J. Teel, R. G. Kope, and R. S. Waples. 1995. Status review of Coho salmon from Washington, Oregon, and California. United States Department of Commerce. National Oceanic and Atmospheric Administration, Technical Memorandum NMFS-NWFSC-24, Seattle, Washington and Long Beach, California, USA.
Wells, J. V., and M. E. Richmond. 1995. Populations, metapopulations, and species populations: what are they and who should care? Wildlife Society Bulletin 23:458–462.
Wilson, E. O. 1994. Naturalist. Island Press, Washington, D.C., USA.
Wilson, E. O., and W. L. Brown. 1953. The subspecies concept and its taxonomic applications. Systematic Zoology 2:97–122.
Wright, S. 1978. Evolution and the genetics of populations. Volume 4. University of Chicago Press, Chicago, Illinois, USA.
Zink, R. M. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. Proceedings of the Royal Society of London, Series B, 271:561–564.
Zink, R. M., G. F. Barrowclough, J. L. Atwood, and R. C. Blackwell-Rago. 2000. Genetics, taxonomy, and conservation of the threatened California gnatcatcher. Conservation Biology 14:1394–1405.

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