Designatable Units for Status Assessment of Endangered Species

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Abstract: *Species status assessment and the conservation of biological diversity may require defining units below the species level to portray probabilities of extinction accurately and to help set priorities for conservation efforts. What those units should be has been debated in the scientific literature largely in terms of evolutionarily significant units (ESUs), but this discourse has had little impact on government policy with regard to status assessment. As with species concepts, the variously proposed ESU concepts have not been resolvable into a single approach. The need for a practicable procedure to identify infraspecific entities for status assignment is the motivation behind employing designatable units (DUs). In aid of a policy to prevent elements of biodiversity from becoming extinct or extirpated, DUs are determined during the process of resolving a species' conservation status according to broadly applicable guidelines. The procedure asks whether putative DUs are distinguishable based on a reliably established taxonomy or a well-corroborated phylogeny, compelling evidence of genetic distinction, range disjunction, and/or biogeographic distinction as long as extinction probabilities also differ. The language of the DU approach avoids wording that implies value judgments concerning evolutionary importance or significance. Because species conservation status assessment is not science but, rather, the use of science to further policy, DUs contribute to a precautionary approach to listing whereby status may be assessed even though knowledge of systematic relationships below the species level may be lacking or unresolved. The pragmatic approach of using DUs has been adopted by the Committee on the Status of Endangered Wildlife in Canada for status assessment of species under the Canadian Species at Risk Act.*

Key Words: conservation policy, COSEWIC, distinct population, Endangered Species Act, evolutionarily significant unit, extinction risk, Species at Risk Act

Unidades Designatables para la Evaluación del Estatus de Especies en Peligro

Resumen: *La evaluación del estatus de especies y la conservación de la diversidad biológica puede requerir de unidades debajo del nivel de especie para delinear las probabilidades de extinción con precisión y ayudar a definir prioridades para los esfuerzos de conservación. La identidad de esas unidades se ha debatido en la literatura científica principalmente en términos de unidades evolutivas significativas (UES), pero este discurso ha tenido poco impacto en las políticas gubernamentales en relación con la evaluación de estatus. Como con el concepto de especie, los diversos conceptos de UES que se han planteado no son resolubles en un solo método. La necesidad de un procedimiento viable para identificar entidades infraespecíficas para la asignación de estatus es la motivación para el uso de unidades designatables (UD). En apoyo a una política para prevenir que elementos de la biodiversidad se extingan o sean extirpados, los UD son determinados conforme a directrices ampliamente aplicables durante el proceso de resolución del estatus de conservación de una especie. Este proceso pregunta si UD putativas son distinguibles con base en una taxonomía establecida confiablemente o en una filogenia bien corroborada, en evidencia convincente de la diferenciación genética, de la disyunción de rango, y/o de diferenciación biogeográfica, siempre que las probabilidades de extinción también difieran. El lenguaje del método de las UD evita el fraseo que implica juicios de valor referentes a la importancia o significado evolutivo. Debido a que la evaluación del estatus de conservación no es ciencia, sino, más bien, el uso de ciencia para favorecer políticas, las DU contribuyen a un acercamiento precautorio al enlistado con el cual se puede evaluar el estatus aun cuando el conocimiento de las relaciones sistemáticas debajo del nivel de*

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especies este ausente o no resuelto. El método pragmático que utiliza los DU ha sido adoptado por el Comité Canadiense para el Estatus de la Vida Silvestre en Peligro para evaluar el estatus de especies en el marco del Acta Canadiense de Especies en Riesgo.

Palabras Clave: Acta de Especies en Peligro, Acta de Especies en Riego, COSEWIC, población distinta, políticas de conservación, riesgo de extinción, unidad evolutiva significativa

Introduction

To conserve and protect biological diversity, conservation biologists, wildlife managers, and environmental policy makers must have effective means to recognize and assess the conservation status of endangered or threatened species. The assessments need to be done according to principles that are consistent and defensible. Invariably, species that are at risk of extinction must be officially listed in some manner for protection and recovery measures to be implemented. To that end, populations below the species level may need to be considered when appropriate. Species' ranges are genetically, demographically, spatially, and ecologically heterogeneous in ways that current taxonomies may or may not capture. Accordingly, Section 3(15) of the 1973 U.S. Endangered Species Act (ESA), as amended in 1978, has provision for listing "distinct population segments" (DPSs) of vertebrate animals by including them in its definition of species. Section 2(1) of the Canadian Species at Risk Act (SARA) of 2002 and Section 528 of the Australian Environment Protection and Biodiversity Conservation Act of 1999 likewise enable the consideration of distinct populations as wildlife species for legal listing.

Despite the understandable value of recognizing distinct populations, an unambiguous definition of what they may be has been elusive. The reason for this resides in the same, inherent uncertainties that beset the many proposals for defining or recognizing species as entities in systematics (Hey et al. 2003). Neither semantics nor systematics is, however, the real issue. The purpose for recognizing distinct populations is the appropriate assessment of conservation status so that suitable actions may be subsequently undertaken (Mace 2004). Neither the ESA nor SARA provides direction on how to interpret their distinct population provisions; therefore, there is need for guidance to implement this policy. I present a methodology that is now in use by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) under the aegis of SARA and give examples of its application for amphibians and other vertebrates that are at risk.

Evolutionarily Significant Units

In the scientific literature, DPSs have largely been equated with evolutionarily significant units (ESUs) as the means to recognize entities below the species level for status assessment and protection. Evolutionarily significant units, as subsets of species possessing "genetic attributes significant for the present and future of the species in question," were proposed by Ryder (1986) to provide an alternative to the use of subspecies. Subsequently, numerous competing criteria for determining ESUs have emerged (Fraser & Bernatchez 2001; Moritz 2002; Waples 2005), the most influential being those of Waples (1991, 1995) and Moritz (1994). Evolutionarily significant units are sometimes readily apparent in species with discrete genetic and geographic subunits, as with populations of anadromous salmonid fishes (Waples 1995; N.K. Johnson et al. 1999), but clarity is not guaranteed (Taylor & Dizon 1999; Crandall et al. 2000). Because mitochondrial genes and nuclear genes accumulate neutral mutations at different rates (Avise 2000), there may be discord between evolutionary units discernible using mtDNA versus nuclear DNA genetic markers (Ferris et al. 1983; Rognon & Guyomard 2003). For example, ESUs proposed for Scandinavian brown bears based on mtDNA variation were not significant when nuclear genetic markers were examined (Waits et al. 2000).

There is a decided lack of consensus surrounding the concept of the ESU (Waples 1998; Bowen 1999; Young 2001). This discord has its roots in the same philosophical and interpretative dilemmas that plague the scientific definition of *species* (Ereshefsky 1991; Sober 1993; Hey 2002), which is a problem afflicted by a scourge of competing concepts, each of which emphasizes a different aspect of the nature of species and criteria for recognizing them (Mayden 1997; Turner 1999; Lee 2003 for compendia). There are altogether too many species concepts. Mayden (1997) listed 22, and more (de Queiroz 1998; O.W. Johnson et al. 1999; Rosselló-Mora & Amann 2001; Wilkins 2003) have emerged since. The various ESU concepts, although mercifully fewer in number than species concepts, echo this dilemma. They, too, conflict over criteria. The ESU, in its many guises, has been variously criticized for insufficiently recognizing evolutionary potential (Bowen 1998), conflating species concepts (Roe & Lydeard 1998), inadequately considering evolutionary processes (Crandall et al. 2000), undervaluing demographic and behavioral data (Pennock & Dimmick 1997), overemphasizing adaptation (Dimmick et al. 1999), and underemphasizing adaptation (Crandall et al. 2000; Fraser & Bernatchez 2001). Use of differing ESU concepts can result in greatly differing numbers of ESUs being recognized within species (Waples 2005). Just as no one species concept has proven universally acceptable among biologists, no one ESU concept has so far prevailed. It has even been argued that the ESU is itself a species concept (Mayden & Wood 1995).

In short, the ESU, and how to define it, has fueled a lively intellectual debate among scientists (Frasier & Bernatchez 2001; Mace 2004), but that discourse has neither particularly aided the preservation of biological diversity nor much advanced beyond the scientific literature. Significantly, U.S. government policy on DPSs (Fay & Nammack 1996) makes little reference to ESUs except with regard to Pacific salmon, for which it applies Waples' (1991) ESU definition. The majority of infraspecific listings under the ESA, except for salmon, are based on subspecies. The scientific debate on ESUs has thus been largely academic.

A Pragmatic Alternative: Designatable Units

Endangered species protection and recovery are too imperative to remain embroiled in debates about definitions and concepts (Agapow et al. 2004). Recognition both of species and of populations below the species level for assessment must be guided by the general objective of preventing elements of biodiversity from becoming extinct or extirpated. This is a policy decision, not a scientific theory or a philosophical axiom. What is needed to fulfill this policy of identifying diversity is a means that is informed by science, not specifically a scientific (i.e., knowledge-seeking) protocol. Legislation does not deal with hypotheses. Scholarly arguments about the adaptive significance, evolutionary potential, or reciprocal monophyly of biological entities have no practical value once the entities concerned have been allowed to go extinct (Daugherty et al. 1990). Thus lack of resolution among scientists concerning the nature of either species or ESUs can be an obstacle in the path of legal statutes concerning the protection of species. Policy on endangered species protection is based on designation of extinction risk status for recognizably distinct biological entities. Hence, laws must themselves define *species* within their areas of jurisdiction, as is true for both the ESA and SARA. Their implementation would benefit from mechanisms for legal recognition of distinct populations designed with species protection policies in mind (Waples 2005).

What are required, therefore, are biologically based units that may be designated based on conservation status, not necessarily taxonomic status, guided by the general policy objective of preventing irreplaceable units of biodiversity from becoming extinct or extirpated from a jurisdiction. These are designatable units (DUs), to be recognized in cases where one status designation encompassing the whole of a species is not sufficient to accurately portray probabilities of extinction within that species.

Evidence of biological distinction—biodiversity in the broadest sense—logically should be the compelling systematic basis for recognizing distinct populations within a species. Conservation policy, though, requires an additional criterion. Thus, the U.S. DPS policies for both salmonid fishes (i.e., Waples' 1991 ESU concept) and other species (Fay & Nammack 1996) are effectively two-part tests. Waples' ESU concept asks, first, if the putative ESU is reproductively isolated and, second, if it is an important component of the evolutionary legacy of the species. For other species, U.S. DPS policy asks if the putative DPS is discrete and if it is significant. In both cases, though, the second question is value laden. Concepts such as "importance" and "significance" are not easily quantifiable. Determining DUs similarly constitutes a two-part test and asks, first, if putative DUs are distinguishable and, second, if they have differing conservation status. This is a distinguishing feature of DUs because status is something that can be estimated without implicit value judgments.

Identifying Designatable Units

Patterns of population structure, life history, and genetic variability differ across taxonomic groups and the extent of knowledge about species varies from case to case. In some instances, information may be available from genetic marker studies but in other cases genetic distinction can only be inferred from morphological, physiological or life-history traits or from geographic distribution. Therefore, what it is that constitutes a distinguishable element of biological diversity needs to be interpreted on a case-by-case basis. This can be aided by a system of guidelines. Guidelines for recognizing DUs (Appendix) consider, in order of precedence, established taxonomy, direct or inferred genetic evidence, range disjunction, and biogeographic distinction, coupled with consideration of conservation status (Fig. 1).

The most obvious form DUs may take is that of recognized subspecies. For example, COSEWIC separately lists Canadian subspecies of the Loggerhead Shrike (*Lanius ludovicianus*) and northern water snake (*Nerodia sipedon*) because they have different status designations. The legitimacy and monophyly of subspecies may be questioned (Zink 2004), but the evolutionary diversification of infraspecific lineages is complex (Pennock & Dimmick 1997; Crandall et. al. 2000; Pearman 2001). Although monophyly, as a criterion, aids understanding of the history of clade origins, especially species and higher taxa, paraphyly and polyphyly are prevalent within species (Funk & Omland 2003). However faulty for certain types of analysis, the naming of subspecies tends to recognize biological

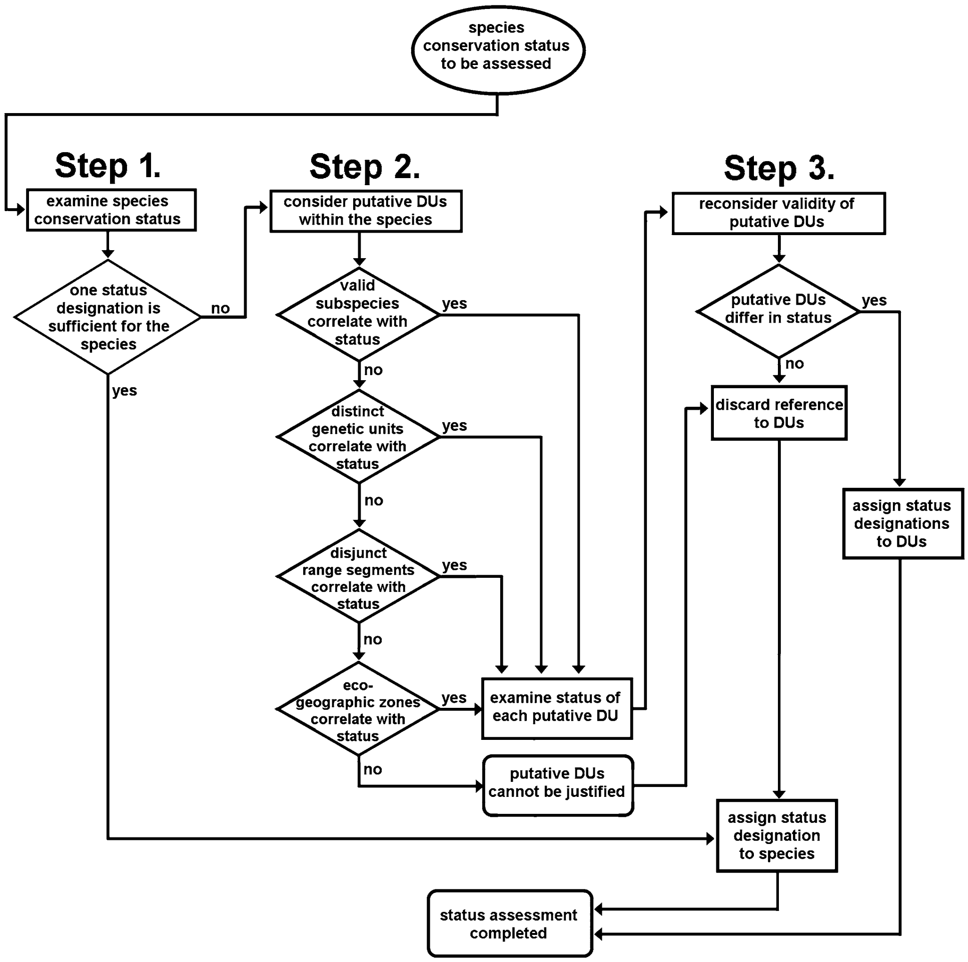

Figure 1. Flowchart of the process for discerning and employing designatable units (DUs) in species status assessment (see Appendix).

distinctiveness at some level and should be sufficient as a first-order systematic hypothesis when the aim of conservation is to preserve biological diversity.

Designatable units may also be identified based on demonstrations of genetic distinctiveness, similar to the recognition of ESUs in the sense of Waples (1991) or Moritz (1994). Evidence may be derived via heritable morphological, life-history, or behavioral traits or neutral genetic markers. Interpreting phylogenetic trees to identify candidate DUs is admittedly problematic because there is no obvious objective criterion for use in deciding how much genetic differentiation is sufficient. The same problem afflicts the recognition of genetically based ESUs (Waples 2005). Drawing a line across a phylogeny at an appropriate hierarchical level requires an additional criterion that, for DUs, is afforded by considering conservation status differences (Fig. 2). Yet this too may not be clear in every case. Because the issue of how and when to use genetic evidence of distinctiveness is most often a matter of opinion, resolution should be based on discussion and consensus in the interests of furthering endangered species protection policy. This is how COSEWIC, as a committee, makes its decisions in such cases.

Disjunctions between substantial portions of a species' global geographic range indicate that dispersal of individuals between those regions is severely limited or impossible. As such, natural range disjunctions are indicators of probable genetic differentiation and therefore, in conjunction with estimations of status, may be used as the basis for recognizing DUs. The relict Nova Scotia population of Blanding's turtle (*Emydoidea blandingi*), for example, is completely isolated from other populations of the same species and has a different probability of long-term survival (Herman et al. 1995).

Finally, occupation of differing biogeographic regions by a species reflects the probable existence of historical or genetic distinctions and adaptations in each of those regions even though the range may appear to be continuous. In northern latitudes, following the Pleistocene glaciation, terrestrial animals with good dispersal abilities, such as birds and large mammals, or plants with small, wind-blown seeds, have formed recognizable biogeographic zones (Ricketts et al. 1999). On the other hand, many smaller, less vagile terrestrial animals, including gastropods, amphibians and reptiles, entered their present northern ranges by following a limited number of

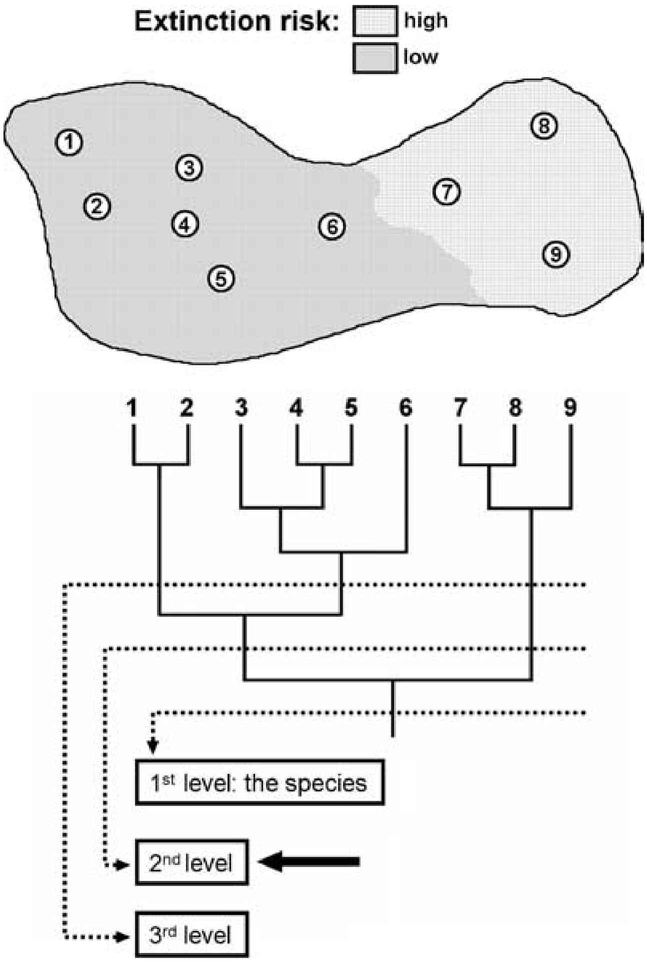

Figure 2. Determination of the appropriate level in a phylogenetic hierarchy at which to recognize designatable units (DUs), with conservation status as an independent criterion. In this hypothetical example, extinction risk is variable across the range of a species, and the phylogenetic relationships of nine populations have been determined. Because extinction risk is not uniform, one status designation encompassing the entire species—the first-level cut of the tree—is not sufficient to accurately portray the probabilities of extinction. The more inclusive second-level cut of the tree (arrow) captures the two levels of extinction risk and therefore is appropriate for designating DUs (one DU consisting of the lineage containing populations 1–6 and other DU consisting of the lineage containing populations 7–9). A further and more inclusive third-level cut of the tree extends across more lineages but does not increase resolution of conservation status.

dispersal corridors (Bos & Sites 2001; Austin et al. 2002; Zamudio & Savage 2003; Hoffman & Blouin 2004). Freshwater fishes and molluscs dispersed according to drainage patterns and emerging watersheds following glacial retreat (Abell et al. 2000). In previously glaciated North America, the tiger salamander (*Ambystoma tigrinum*) has an extensive range, variable conservation status in different parts of that range, and considerable morphological variation. The species is endangered in semidesert interior valleys of southern British Columbia and, evidently, has been extirpated from the Carolinian forest zone of southern Ontario; but it is abundant enough to be considered to be not at risk on the Canadian prairies. The subspecies taxonomy, however, is highly contentious (Shaffer & McKnight 1996; Irschick & Shaffer 1997) and an unreliable basis for status assessment. Designatable units based on the different biogeographic zones the species occupies are the most defensible and prudent means to adequately describe its overall conservation status (Schock 2001). For the northern leopard frog (*Rana pipiens*) in Canada, COSEWIC returned different status assessments for eastern versus prairie and western boreal populations (Seburn & Seburn 1998, 1999). Recently, this distinction has been shown to have a good phylogeographic basis (Hoffman & Blouin 2004).

There are also instances where DUs should not be recognized. Because DUs are used specifically for cases in which one status designation for the entire species is not sufficient, they are not required if all putatively designatable populations have the same status. In such cases, the status designation simply should be applied to the entire species. In the western United States, the five disjunct portions of the range of the bull trout (*Salvelinus confluentus*) have each been recognized as a DPS for the purposes of management; nevertheless, all have the same conservation status (Barry 1999). Distinguishable units would not be recognized for this species. Furthermore, within the jurisdictional limits of a particular law or listing agency, DUs are not local or politically bounded management units. For example, DUs under SARA, a Canadian federal law, are not to be based on provincial borders. Similarly, off the Atlantic coasts of Canada and the United States, the Northwest Atlantic Fisheries Organization recognizes a set of major and minor fisheries management zones but these zones do not necessarily correspond to biological populations. Fisheries stocks managed on the basis of zones such as these should not be eligible for recognition as DUs by either country.

Conclusions

Recognizing conservation status for species at risk of extinction is an action taken in the process of using science in support of policy. The concept of designatable units is intended to aid the implementation of policy and, with that, conservation action and informed management. The recognition of DUs describes a species' conservation status and not necessarily the taxonomic, evolutionary, or phylogeographic significance of any component parts.

Evolutionary patterns therefore are not the focus, and the methodology does not rely on a priori systematics. The use of DUs might be criticized for recognizing "nonevolutionary" units or for not paying strict attention to the demonstration of monophyly, which are criticisms leveled at various versions of the ESU as well. The discovery of real evolutionary and historical entities is the precinct of systematics, which clearly has a vital role to play in identifying those entities (Dimmick et al. 1999; Mace 2004). Contrarily, conservation status is determined based on ecological data, including information on habitat and population trends and threats, according to criteria grounded, for instance, in time-to-extinction models (Mace & Lande 1991; Gärdenfors 2001). Employment of DUs is a pragmatic approach to extinction risk assessment that seeks to avoid serious conceptual and methodological pitfalls of approaches based too exclusively on taxonomic inference.

The concept of DUs has emerged with the needs of the Canadian system of endangered species protection under SARA in mind. In the Canadian system, recognizing and listing an endangered or threatened species is a process that is separate from actions taken toward recovery, including setting priorities for recovery action. Value-laden words such as importance or significance, which can cloud the objective assessment of status, begin to have meaning in the more sociopolitical realm of recovery policy and planning. Canada also has no distinct "delisting" process for recovering species in the same manner as in the United States under the ESA. Under SARA, a species' status is reassessed by COSEWIC about every 10 years based on the same methods and criteria applied in the initial listing. Upon reassessment a species may be reassigned to another status category, including "not at risk," if its condition has altered. Recognition of DUs may also be adjusted upon reassessment. This is desirable because knowledge of systematic relationships and conservation status may change and be better understood in the interim. Finally, COSEWIC assesses only the risk of species loss from Canadian territory, in accordance with the jurisdictional limits of SARA. The loss of a Canadian endemic species, therefore, is an extinction, whereas the loss from Canada of a species that may still exist elsewhere is labeled an extirpation.

Scientists are rightfully prudent to avoid adding false information to the canon of knowledge. They therefore scrupulously avoid the possibility that they might accept a hypothesis that is actually false. If we as scientists are to be wrong, we consider it better to reject a hypothesis even though it may be true. In science this is a sensible and precautionary policy (Taylor & Dizon 1999). But recognizing and listing endangered species is not science. It is an aspect of environmental and conservation policy that is best guided by the results of science. The ultimate consequence of failing to safeguard a species that is actually endangered (i.e., the error of rejecting a hypothesis of endangerment even though it may be true) is dire and irreversible. In conservation practice, unlike the practice of science, we must avoid that sort of error and be careful not to lose potentially unrecognized species from the canon of life. Indeed, the Canadian Species at Risk Act (Preamble and Section 38) enunciates the precautionary principle that ". . . measures to prevent the reduction or loss of the species should not be postponed for a lack of full scientific certainty." If we as conservationists are to be wrong, we must consider it better to accept a hypothesis of risk even though it may be false. The DU approach is likewise precautionary in the same sense.

Notwithstanding differing opinions concerning what ideally should be the objects of conservation science and policy, a species under law is what is legislated, not what is discovered. Scientists should be mindful of this distinction or their advice will be ignored. Species concepts and biological distinctions do matter, thus taxonomy is indispensable for conservation (Mace 2004). Yet there is much biodiversity under threat, not much time, and not nearly enough money. Agapow et al. (2004) decry the "terrible ambiguity of species" with reference to conservation of biodiversity in that a simple and universally applicable concept of species boundaries may never be forthcoming. They argue that a flexible spectrum of methodologies and workable guidelines are needed, not only for scientists but also for legislators, policy makers, and the general public. The idea of DUs, for the single purpose of categorizing variable probabilities of extinction risk within a species, across its range, and within a jurisdiction, is a proposal with those needs in mind.

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Appendix

Protocol and guidelines for recognizing designatable units (DUs) in accordance with the practice of the Committee on the Status of Endangered Wildlife in Canada.

Step 1. Examine the species as a whole.

If a single, uniform status rank is appropriate to accurately portray the probability of extinction of the species, proceed to assess the status of the species. Alternatively, if there are significant subdivisions within the species such that a single status designation may not be sufficient to accurately portray probabilities of extinction within the species, proceed to examine the status of putative DUs below the species level.

Step 2. Identify and assess putative DUs.

Units to which status may be assigned below the species level are recognized as DUs on the basis of any one of the following four biologically based criteria, in order of precedence. DUs should not be recognized for management units that are not rooted in biologically based criteria (i.e., arbitrarily or politically delineated management zones and subjurisdictional political boundaries such as county lines or state and provincial borders).

A. Named subspecies or varieties, as listed in an appropriate standardized faunal or floral checklist, are eligible for recognition as DUs. Where no standardized taxonomic list is available, taxa currently recognized by relevant scientific authorities are open to consideration.
B. Genetically distinct units, based on appropriate, inherited morphological, life history, or behavioral traits and/or genetic markers such as allozymes, DNA microsatellites, DNA restriction fragment length polymorphisms (RFLPs), or DNA sequences might be recognized as DUs.
C. Substantial portions of a species' global geographic range that are separated by a major natural range disjunction may be DUs. The disjunction must ensure that dispersal of individuals between separated regions has been severely limited for an extended period of time and is not likely in the foreseeable future.
D. Biogeographically distinct units that occupy differing ecogeographic regions (e.g., the coniferous boreal forest versus the central prairies of North America) which are relevant to the species and reflect historical or genetic distinction may be DUs. Appropriate, large-scale ecozone or biogeographic-zone maps are useful for recognizing these DUs.

Step 3. Reassess putative DUs according to need and validity.

If all putative DUs have the same status designation, the status designation should be applied to the entire species as one unit and reference to DUs should be dropped.