# **Quantification of Extinction Risk: IUCN's System for Classifying Threatened Species**

GEORGINA M. MACE,\*§§ NIGEL J. COLLAR,† KEVIN J. GASTON,‡
CRAIG HILTON-TAYLOR,§ H. RESIT AKÇAKAYA,\*\* NIGEL LEADER-WILLIAMS,††
E.J. MILNER-GULLAND,\* AND SIMON N. STUART‡‡

\*Centre for Population Biology and Division of Biology, Imperial College London, Silwood Park, Ascot SL5 7PY, United Kingdom †BirdLife International, Wellbrook Court, Girton Road, Cambridge CB3 0NA, United Kingdom

‡Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom

§Red List Unit, IUCN Species Programme, IUCN UK Office, 219c Huntingdon Road, Cambridge CB3 0DL, United Kingdom \*\*Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794, U.S.A.

††Durrell Institute of Conservation and Ecology, Department of Anthropology, Marlowe Building, University of Kent, Canterbury CT2 7NR, Kent, United Kingdom

‡‡IUCN/SSC - CI/CABS Biodiversity Assessment Unit, IUCN Species Programme, c/o Conservation International, 2011 Crystal Drive, Arlington, VA 22202, U.S.A.

Abstract: The International Union for Conservation of Nature (IUCN) Red List of Threatened Species was increasingly used during the 1980s to assess the conservation status of species for policy and planning purposes. This use stimulated the development of a new set of quantitative criteria for listing species in the categories of threat: critically endangered, endangered, and vulnerable. These criteria, which were intended to be applicable to all species except microorganisms, were part of a broader system for classifying threatened species and were fully implemented by IUCN in 2000. The system and the criteria have been widely used by conservation practitioners and scientists and now underpin one indicator being used to assess the Convention on Biological Diversity 2010 biodiversity target. We describe the process and the technical background to the IUCN Red List system. The criteria refer to fundamental biological processes underlying population decline and extinction. But given major differences between species, the threatening processes affecting them, and the paucity of knowledge relating to most species, the IUCN system had to be both broad and flexible to be applicable to the majority of described species. The system was designed to measure the symptoms of extinction risk, and uses 5 independent criteria relating to aspects of population loss and decline of range size. A species is assigned to a threat category if it meets the quantitative threshold for at least one criterion. The criteria and the accompanying rules and guidelines used by IUCN are intended to increase the consistency, transparency, and validity of its categorization system, but it necessitates some compromises that affect the applicability of the system and the species lists that result. In particular, choices were made over the assessment of uncertainty, poorly known species, depleted species, population decline, restricted ranges, and rarity; all of these affect the way red lists should be viewed and used. Processes related to priority setting and the development of national red lists need to take account of some assumptions in the formulation of the criteria.

Keywords: conservation priority setting, extinction risk, IUCN Red List, threatened species

Cuantificación del Riesgo de Extinción: Sistema de la UICN para la Clasificación de Especies Amenazadas

**Resumen:** La Lista Roja de Especies Amenazadas de la UICN (Unión Internacional para la Conservación de la Naturaleza) fue muy utilizada durante la década de 1980 para evaluar el estatus de conservación de

§§email g.mace@imperial.ac.uk Paper submitted January 11, 2008; revised manuscript accepted April 28, 2008.

especies para fines políticos y de planificación. Este uso estimuló el desarrollo de un conjunto nuevo de criterios cuantitativos para enlistar especies en las categorías de amenaza: en peligro crítico, en peligro y vulnerable. Estos criterios, que se pretendía fueran aplicables a todas las especies excepto microorganismos, eran parte de un sistema general para clasificar especies amenazadas y fueron implementadas completamente por la UICN en 2000. El sistema y los criterios han sido ampliamente utilizados por practicantes y científicos de la conservación y actualmente apuntalan un indicador utilizado para evaluar el objetivo al 2010 de la Convención de Diversidad Biológica. Describimos el proceso y el respaldo técnico del sistema de la Lista Roja de la IUCN. Los criterios se refieren a los procesos biológicos fundamentales que subyacen en la declinación y extinción de una población. Pero, debido a diferencias mayores entre especies, los procesos de amenaza que los afectan y la escasez de conocimiento sobre la mayoría de las especies, el sistema de la UICN tenía que ser amplio y flexible para ser aplicable a la mayoría de las especies descritas. El sistema fue diseñado para medir los síntomas del riesgo de extinción, y utiliza cinco criterios independientes que relacionan aspectos de la pérdida poblacional y la declinación del rango de distribución. Una especie es asignada a una categoría de amenaza si cumple el umbral cuantitativo por lo menos para un criterio. Los criterios, las reglas acompañantes y las directrices utilizadas por la UICN tienen la intención de incrementar la consistencia, transparencia y validez de su sistema de clasificación, pero requiere algunos compromisos que afectan la aplicabilidad del sistema y las listas de especies que resultan. En particular, se bicieron selecciones por encima de la evaluación de incertidumbre, especies poco conocidas, especies disminuidas, declinación poblacional, rangos restringidos y rareza; todas estas afectan la forma en que las listas rojas deberían ser vistas y usadas. Los procesos relacionados con la definición de prioridades y el desarrollo de las listas rojas nacionales necesitan considerar algunos de los supuestos en la formulación de los criterios.

Palabras Clave: definición de prioridades de conservación, especies amenazadas, Lista Roja UICN, riesgo de extinción

# Introduction

In 1994 a new set of rules was adopted by the International Union for Conservation of Nature (IUCN) for listing species in red lists of threatened species and in red data books. The IUCN based these rules on Mace and Lande (1991), incorporating a set of quantitative criteria to be used for classifying species into the categories of threat. These rules and the criteria have been widely applied since 1994, there have been periodic reviews and adjustments made to them, and guidelines have been developed for their application at global, regional, and national levels. The system has been stable since 2001 and increasingly adopted as a standard for the classification of threatened species. Despite the extensive use of the new red list criteria and the publicity that the release of each new IUCN Red List attracts, some common misunderstandings are held about the purpose and nature of the IUCN Red List and the way categorizations arising from it can and should be used in wider planning and legislative processes. Consequently, this paper has 3 aims. First, to present the structure and function of the IUCN system and outline its philosophical and technical background. Second, to clarify some widely misunderstood aspects of the IUCN system, both in terms of its intent and the basis for the categories and criteria. Third, to further increase understanding of the IUCN Red List in advance of its use as one of the measures for the CBD 2010 biodiversity target.

# **Development of IUCN Red List Categories**

#### **Brief History of the IUCN Red List**

Since the 1950s IUCN has compiled lists of species at risk of extinction. These lists gained wide currency in the early 1960s through international red data books for birds and mammals (Fitter & Fitter 1987), which were used widely in scientific, political, and popular contexts as a means of highlighting the world's most threatened species. The IUCN Red Data Book program became increasingly comprehensive in the 1970s and sought to include all higher vertebrates and representative groups of fishes, invertebrates, and plants. Categories were developed to subdivide extinction risk that reflected the degree of threat and uncertainty and included, for example, endangered, vulnerable, rare and indeterminate, insufficiently known, and out of danger. These early attempts to develop a threat-classification system confounded several issues, such as the severity of the threat; likelihood of extinction; causes of threat, such as overhunting or habitat loss; and the nature of population vulnerability, such as a small fragmented population or a single large one. Furthermore, the definitions of these categories depended on subjective perceptions and thus were vulnerable to skepticism, uncertainty, and controversy, particularly when commercial interests were at stake or species conservation issues stimulated strongly held opinions and emotions.

As a result the rules for assessing threat status and for classifying species into the red list categories came into question in the 1980s. Consistency was initially achieved by individual compilers who worked with the taxon specialist groups of IUCN and International Council for Bird Preservation (ICBP; now BirdLife International) to reach a consensus on the conservation status of taxa. In 1980 IUCN established the Conservation Monitoring Centre with a group of compilers who used a common base of information on environmental circumstances and adopted a standard approach to status assessments. This initiative began to collapse by the late 1980s (Collar 1996) even though the need for comprehensive, reliable lists of globally threatened species was growing. The IUCN then devolved responsibility for listing species to their networks of experts, but recognized that reduced consistency in applying its subjective categories of threat was likely to result. Moreover, from 1986 onwards, the red data books (apart from those for birds) were gradually replaced by a simple red list of species that contained no detailed information, thereby opening a huge gap in the information base on which to justify the designation of a species as threatened.

In 1984 a review of the red data categories (Fitter & Fitter 1987) identified the pressing need for a more robust, objective, and widely applicable system, and led to the IUCN Species Survival Commission (SSC) Steering Committee inviting a group of scientists to prepare a discussion paper for circulation within IUCN. This stimulated a proposal for the threat categories critical, endangered, and vulnerable and quantitative criteria for each one (Mace & Lande 1991). Following discussion and review within IUCN, the categories were incorporated into a wider set of rules, and the system was adopted in 1994 (IUCN 1994). The new IUCN Categories and Criteria were first applied to birds (Collar et al. 1994) and then used for the 1996 IUCN Red List of Threatened Animals (IUCN 1996). The system was reviewed during 1997-2000 (Mace 2000), and a somewhat modified set of rules were adopted by IUCN Council in 2000 (IUCN 2001). There have been no changes since then.

#### **Purpose of Red Listing**

Red lists were intended to raise awareness and to help direct conservation actions for species (Fitter & Fitter 1987). The IUCN (1996) states that the goals of its red list are to (1) provide a global index of the state of degeneration of biodiversity and (2) identify and document those species most in need of conservation attention if global extinction rates are to be reduced. To meet these goals, the classification system must be objective and transparent. It also needs to be applicable to a variety of species and habitats; standardized to yield consistent results independent of the assessor or the species being assessed; accessible to allow a variety of species experts to use it;

scientifically defensible; and reasonably rigorous (i.e., it should be hard to classify species inappropriately).

# Criteria Development 1991–1995

Mace and Lande's (1991) proposal outlined some fundamental objectives for a new system and the background rationale for 3 categories reflecting increasing levels of risk over decreasing timescales. The categories were defined precisely in terms of extinction risk, but a set of criteria was developed on the basis of population sizes, population fragmentation, and observed or projected declines in abundance that equated approximately to that level of risk.

This proposal was intended for review and development, but was immediately applied to various taxa, particularly through workshops organized by the Captive (now Conservation) Breeding Specialist Group of the IUCN SSC (Seal et al. 1994), and several bird and plant groups (Osborne 1995; Green 1996; McGowan & Gillman 1997). A proposal was also made to extend the new system for listing species in the Appendices to the Convention on International Trade in Endangered Species (CITES). Consequently, the SSC decided that further work was needed to test and validate Mace and Lande's (1991) proposals and to broaden their applicability. During 1992 comments were sought from various experts, and 2 workshops were held in November 1992 to review the proposals and their development. At the end of the workshops, 4 sets of draft criteria for threatened status had been prepared, appropriate to the major taxonomic groupings of invertebrates, vertebrates, plants, and fishes. A small drafting group was appointed by SSC to continue the process (Mace et al. 1992).

Reviewing the taxonomically based criteria revealed some interesting differences and parallels. In terms of differences, the working groups on vertebrates tended to focus on population size and structure, whereas working groups on plants emphasized geographic distribution area and life-history attributes and invertebrate biologists focused on population fluctuations and habitat fragmentation. There was much overlap between alternative sets of criteria. All working groups considered some form of continuing population decline an indicator of threatened status. Furthermore, there was evidence that some criteria developed with one taxonomic group in mind could be relevant to another, depending on their life histories and the threats each faced. Criteria developed for vertebrates, for example, could sometimes be more appropriate than those developed for plants, particularly in the case of species such as trees or cycads that are relatively long-lived and individually identifiable.

Therefore, the alternative criteria were merged into a single set to be applied to all species. Biologically, this reflects the different ways in which extinction risk may be expressed. Taxa with similar life forms and life histories

may express extinction risk by just 1 or 2 of these, but because there are exceptions it is judicious to allow species to be evaluated against all criteria. Thus, long-lived trees that can be identified individually may share extinction risk traits with large vertebrates, whereas small, spawning fishes may have extinction-risk traits in common with annual or biannual plants. The decision to adopt a single set of criteria for all species does not imply that all species are directly comparable in terms of the evidence for being at elevated extinction risk. Instead, the multiple criteria can be regarded as a series of alternative sets of symptoms, any of which might be appropriate regardless of the taxonomic affiliation of the species.

The first version of the criteria was reviewed by workshop participants in February 1993, and after some further revisions, the proposal (now called version 2.0) was published (Mace et al. 1992 [publication is dated 1992, but it was printed and distributed in mid-1993]) and circulated to all 7000 SSC members with a request for comments. A number of taxon specialist groups also undertook a more formal test of the criteria, providing results compared with other methods and commenting on easeof-use and applicability. By the end of August 1993, over 70 sets of comments and responses had been received, including trial results from application of the draft criteria to over 500 species from many taxonomic groups, including bryophytes, orchids, cacti, cycads, conifers, molluscs, damselflies, dragonflies, butterflies, freshwater fishes, turtles, crocodiles, waterfowl, African primates, equids, sheep, and goats. During September and October 1993, the drafting group and others met to review these comments.

A revision of the criteria was prepared toward the end of 1993 (version 2.1) (IUCN 1993). This was circulated to all IUCN members and was presented at the IUCN General Assembly in January 1994. Feedback from IUCN members and from elsewhere continued throughout early 1994, and more revisions were made for a final version (version 2.2: Mace & Stuart 1994). This version was very close, although not identical, to that finally accepted by IUCN in 1994 and was used for the preparation of *Birds to Watch 2* (Collar et al. 1994). The version accepted by IUCN Council (version 2.3) was published as a booklet (IUCN 1994 [publication is dated 1994, but it was printed and distributed in March 1995]) and includes the formal descriptions of categories, criteria, rules, and definitions.

The 1996 IUCN Red List of Threatened Animals was derived from the new criteria. Over 15,000 species were assessed, of which 5,205 were classified as threatened. At that time there were well-developed processes for assessing birds (BirdLife International) and mammals (an IUCN-led comprehensive review). Nevertheless, the assessment of other animal and plant groups was patchy and unsystematic.

At the same time, IUCN was working to assess the applicability of the new criteria to a diverse set of other taxa, including lower plants, trees, and marine fishes. The work on marine fishes was begun at a specialist workshop at which over 100 species were assessed (Hudson & Mace 1996) for the 1996 IUCN Red List (IUCN 1996). They included some common fisheries species such as Atlantic cod (Gadus morbua), southern bluefin tuna (Thunnus maccoyi), and Atlantic halibut (Hippoglossus hippoglossus), which were listed as threatened because of their recent marked population declines. These listings proved highly controversial (Matsuda et al. 1997). Discussions on the role of the red list and the nature of the criteria at the first World Conservation Congress culminated in a resolution calling on IUCN to complete its review of the general effectiveness of the criteria and to pay particular attention to "(1) marine species, particularly fish, taking into account the dynamic nature of marine ecosystems, (2) species under management programmes, and (3) the time periods over which declines are measured." The IUCN was asked to complete the review by the time of the subsequent World Conservation Congress (2000).

#### Review of the IUCN Criteria 1996–1999

A scoping workshop with about 40 participants, representing different interests and specializations, identified the major issues for the review: (1) range areas of species and the spatial scale of area-based measures, (2) assessment of marine species, (3) regional and national listing, (4) use of population declines for threat assessment, and (5) more specific topics such as measuring uncertainty, definitions of key terms, and the presentation of rules (see http://www.iucn.org/themes/ssc/redlists/techdocs. htm). Between 1998 and 1999, topic-based workshops were held in 6 countries to consider these issues and derive consensus recommendations. Each workshop included representatives from the scoping workshop to ensure continuity and to ensure participation of specialists with regional, topical, or technical expertise. Consensus was reached on all issues at a final workshop held in July 1999, and a set of changes were made to the criteria (Mace 2000). The new criteria (now called version 3.1) were formally adopted by IUCN's Council in February 2000, published (IUCN 2001), and first applied in the 2002 IUCN Red List (IUCN 2002).

#### Wider Application 2000–2004

Following publication of the 2000 IUCN Red List, several related processes were initiated. One of these centered on regional listing. The main IUCN Red List system is primarily designed for application at the global level to entire species, subspecies, or other taxonomic units below the level of species. Nevertheless, since red lists were first published, there has been demand for a system that can be applied within countries or other defined areas.

The criteria as drafted could not be applied directly to subsets of species' ranges because the critical thresholds would then be applied to areas limited by political boundaries that do not necessarily relate to viability of a species (Gärdenfors 1996; Gärdenfors et al. 1999). The IUCN began to develop regional guidelines in 1996, and there has been a continuing process of development, review, refinement, and further review (Gärdenfors et al. 1999, 2001; Gärdenfors 2001) since their formal adoption in 2003. With increased use of IUCN rules for national red lists, discussions have now begun on improved 2-way flows of information between global and national assessments (Miller et al. 2006, 2007).

A second outcome from the 2000 IUCN Red List was the formation of a Red List Partnership whereby organizations with an interest in and commitment to red listing agreed to work with IUCN. In late 2000, IUCN, Conservation International, BirdLife International, and Nature-Serve agreed to form a Red List Partnership. Now active, the partnership was responsible for the production of the first Global Species Assessment in 2004 (Baillie et al. 2004) and for a series of large-scale species assessments (e.g., Global Amphibian Assessment, Stuart et al. 2004; IUCN et al. 2006). During this period there have also been a number of reviews and assessments of the role and effectiveness of the IUCN Red List Criteria, which have helped further define their uses and misuses (Possingham et al. 2002; Harcourt & Parks 2003; Lamoreux et al. 2003; O'Grady et al. 2004; Regan et al. 2005; Akçakaya et al. 2006; de Grammont & Cuaron 2006; Rodrigues et al. 2006).

# Technical Background to the Criteria

#### **Extinction Theory**

The IUCN Red List categories are intended to reflect the likelihood of a species going extinct under prevailing circumstances. Extinction occurs when the mortality (and emigration) rate is greater than the birth (and immigration) rate for a sufficiently long time that the population size reaches zero. All other things being equal, the probability of extinction is greater when the population size is small, when the decline rate is high (death rates are much greater than birth rates), and when fluctuations in population size are large in relation to the population growth rate (increasing the likelihood that the population size reaches zero). Very small populations are susceptible to demographic stochasticity, whereby random variations in birth and death rates can lead to extinction even when the average population growth rate is positive (Richter-Dyn & Goel 1972; Goodman 1987). In addition, small populations can suffer disproportionately from genetic effects, such as accumulation of recessive deleterious alleles under inbreeding (Soulé 1980), loss of quantitative characters that allow adaptation, accumulation of mildly deleterious mutations (Hedrick 1992; Frankham 1995a), and various other behavioral, social, and demographic factors collectively known as Allee effects (Courchamp et al. 1999). In contrast, larger populations are vulnerable when extrinsic threats or processes are driving declines or significant fluctuations from which the populations cannot recover. This distinction was characterized by Caughley (1994) as the small population paradigm and the declining population paradigm; concepts that provided a critical line of thinking in formulating the extinction-risk criteria and particularly in reinforcing the importance of reflecting both types of population vulnerability.

From basic theory it is possible to draw broad generalizations about the relationships among population size, population growth rates, fluctuations in population growth rates, and extinction times (Lande 1993) (Fig. 1). Deterministic exponential declines are always serious, with population size having little effect on extinction risk. Demographic stochasticity is unlikely to be important for any population that has more than about 100 individuals, but random environmental variation or catastrophes are important for populations of all sizes and become more significant as the variation becomes large in relation to the population growth rate. Accumulation of deleterious recessive alleles poses a genetic risk; thus, to safeguard genetic variability over hundreds of years, it is recommended that minimum effective population sizes of at least 50 be maintained. Because the genetically effective population size is frequently <10% of the actual number of individuals in a population (Frankham 1995b), this suggests an absolute minimum population of 500 individuals

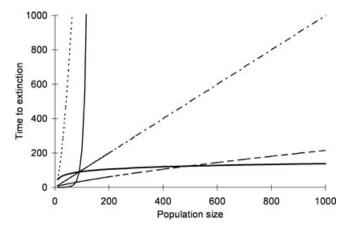


Figure 1. Comparison of the relationship between extinction time and population size under demographic stochasticity (solid line), deterministic decline at r=-0.05 (heavy solid line), and environmental variation in which environmental variance =0.05 and r=0.04 (dashed line), r=0.05 (dashed and dotted line), and r=0.06 (dotted line).

is necessary to avoid deleterious inbreeding. Even larger populations are needed to preserve quantitative trait variation: to maintain high levels (>90%) over thousands of years requires minimum effective population sizes of at least 5000 and to prevent the accumulation of mildly deleterious mutations over tens of thousands of years requires minimum effective population sizes of around 10,000-100,000 (Lynch & Blanchard 1998; Lynch & Lande 1998; Frankham 1999). Because of difficulties in estimating key parameter values, these critical population sizes are best interpreted as guides to the relative importance of different characteristics rather than real thresholds for management (Lande 1998).

Application of this theory to real-world situations is complicated by variation in threats over time and space and by significant differences between species. The IUCN Red List categories are intended to reflect the likelihood of a particular species going extinct under prevailing circumstances; the likelihood of extinction then depends on the threatening processes involved and the characteristics of the species.

#### **Threatening Processes and Species Differences**

The major processes now driving species extinction are of anthropogenic origin and result from habitat loss and alteration, overexploitation, biotic exchange, introduced species, pollution, climate change, and the interactions between these (Diamond 1984; Sala et al. 2000; Millennium Ecosystem Assessment 2005; Thuiller 2007). Understanding the impacts of threat processes is critical to assessing extinction probabilities because they may change nonlinearly with increasing human population growth and development, and their future trajectories and impacts vary with time and place.

Differences in life history, ecology, and behavior among species have significant influences on extinction risk. Extinction-prone species have particular characteristics, such that local extinction tends to be higher for species with restricted ranges, that occupy a small number of sites, or that have low abundances, high temporal population variability, and poor dispersal (Purvis et al. 2000; Fisher & Owens 2004). Although of great significance, simple measures of population size or geographic range may have low predictive power. For example, a simple population count would fail to reflect the difference between a species with no recruitment in which all individuals are aging adults and that might therefore be destined for imminent extinction compared with a population of the same size with continuing recruitment and a balanced age structure. A small range area might have very different consequences for a species in which all individuals occur in one location than for a species that occupies a network of sites that provides a resilient metapopulation structure. Therefore, although the quantitative criteria are defined according to general theory,

measures used to assess a particular species against the criteria are adjusted to account for a species' biological characteristics.

The adjustments are made through the use of customized definitions for biological variables used in the criteria (IUCN 2001, 2006). For example, the population size measures are defined very specifically, adjusting the observed value to reflect the number of mature individuals after accounting for the effects of age, sex, breeding structure, and the degree of populationsize fluctuation. This will approximate to a measure of the genetic or demographic effective population size (Frankham 1995b). Equivalently, time-based measures in the criteria are scaled for the different rates at which taxa survive and reproduce, and generation length is used to provide this scaling. In the criteria, timescales are set to generations when they relate to biological processes. Other key measures that are specifically designed to provide this standardization across very different species concern subpopulation, location, population decline, range area, and fragmentation, all of which are also specifically defined (IUCN 2001).

The interaction between threatening processes and biological traits is also important. For example, the stability of fluctuating populations is reduced by exploitation (Beddington & May 1977). Persecution and introduced predators increase the extinction risk in largebodied birds, whereas habitat loss increases extinction risk for small-bodied habitat specialists (Owens & Bennett 2000). Primates with low ecological flexibility are especially vulnerable to forestry (Isaac & Cowlishaw 2004); land-bridge island reptiles are more likely to go extinct if they have low abundance and high habitat specialization (Foufopoulos & Ives 1999); and extinction of carnivores within reserves is higher for those with large home ranges (Woodroffe & Ginsberg 1998). In addition, previous exposure to a particular threat will render a community more resilient, simply because the susceptible components will have already been lost ("extinction filters"; Balmford 1996).

There is therefore a complicated set of interacting factors determining extinction risk that are impossible to simplify. Furthermore, the driving processes often dominate extinction risks (Simberloff 1986; Harcourt 1995), so it is more relevant to base the assessment of risk on symptoms rather than theoretically derived thresholds. Consequently, detection of symptoms is the basis for the criteria, not causes or consequences, and the system uses the symptoms to classify species into threat categories. This may best be seen as analogous to initial decisions in a hospital emergency department. In both situations, the first priority is to distinguish the cases that need urgent attention. Diagnosis of the nature of the problem and the design of a restorative cure can follow and are best done by appropriate specialists (Mace & Hudson 1999). After accounting for biological differences, species with

the same symptoms (e.g., the same effective rate of decline, population size, range area) are listed at the same threat level, regardless of the amount of information available. This is appropriate because uncertainty or lack of knowledge about drivers or causes of decline should not cause that species to be listed in a lower category of threat.

# The IUCN Red List Categories and Criteria

The IUCN criteria are intended for species and subunits of species. Here we used species to simplify the text, but in all cases the unit for assessment could be a subspecies. A species can be classified into one, and only one, of the categories. The branching points in Fig. 2 denote 3 different classification systems. The first dichotomy is between the category not evaluated and all the other categories. Not evaluated is for species for which no classification has been undertaken. Its use reduces confusion over the status of species in assessed groups that are not included in threat categories, which might otherwise be either not threatened or not evaluated.

The second dichotomy in Fig. 2 is between species for which a threat category has been determined and those for which the information to make any such assessment is lacking (data deficient [DD]). Data deficient is not a category of threat because the information available about the species is too limited to distinguish among threatened and nonthreatened categories (IUCN 2001). Nevertheless, the precautionary recommendation is that DD species should be afforded the same degree of protection as threatened species, at least until more information is forthcoming. It is tempting to think DD means little is known about a species, but this is not necessarily the case. Instead, DD may reflect how little is known about

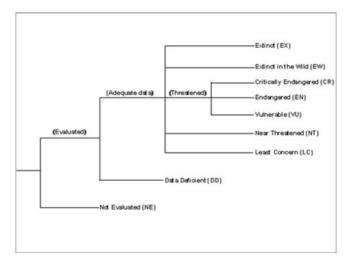


Figure 2. Schematic representation of the IUCN Red List scheme.

processes affecting the species. For example, a species whose biology is very well known from detailed studies at a single location could be classified as DD if the global range or threatening processes are unknown. Conversely, a species restricted to and dependent on one location or habitat type that is under threat could be assessed as at risk even if almost nothing is known about the biology of the species.

The third dichotomy in Fig. 2 reflects the main purpose of the system: the determination of threat level. There are 2 categories for extinct species: extinct (EX) and extinct in the wild (EW), but the definition of extinction is the same for both. Unlike some definitions of extinct, which reflect the time since individuals of the species were last seen, the red list assessment of extinct is strongly influenced by whether surveys have taken place at appropriate times and places. Therefore, it is possible for species to be categorized as EX (or EW) very soon after living individuals have last been observed, but only if there is good evidence that they cannot still persist. Nevertheless, the intention is generally to be extremely precautionary about categorizing taxa as EX or EW. An erroneous extinction classification can have several unfortunate consequences. It can bring the list into disrepute, but more seriously, it can lead to the "Romeo error," whereby a species is believed to be extinct so conservation funding, habitat protection, and even surveys cease before it is really too late (Collar 1998). Inevitably, the EX or EW classification is therefore very conservative and likely to underestimate the number of recent species extinctions. A system to flag critically endangered species that are probably extinct has been proposed as a means to address this problem (Butchart et al. 2006a), and although not formally a part of the IUCN Red List system, it is now included in the documentation requirements.

There are 3 categories representing threat level: critically endangered, endangered, and vulnerable. The categories are defined qualitatively by decreasing probabilities of extinction over increasing timescales and explicitly by 5 criteria (A through E). The categories are nested so that any species that qualifies as endangered must also qualify as vulnerable, and any that qualifies as critically endangered must also qualify as endangered and vulnerable.

To qualify for listing in any of the threat categories, a species needs to meet any 1 of the 5 criteria A through E at that level. Not meeting other criteria has no bearing on an assessment. Criterion E is an extinction risk probability that results from undertaking some kind of quantitative analysis to estimate extinction risk. This criterion is equivalent to the definition of extinction risk in each category used in the Mace and Lande (1991) criteria. The decision to move this from a definition for a category of threat to 1 of 5 criteria was made because of the difficulties in showing that the criteria equated to the extinction-risk probabilities. It was also recognized

that the quantitative assessment of extinction risk could be nonprecautionary, especially if assessors use inappropriate PVA analyses that do not incorporate all relevant risk factors to make an assessment (Akçakaya & Burgman 1995; Beissinger & Westphal 1998; Coulson et al. 2001). The criteria for assignment to a threatened category are discussed further later.

The category least concern is used for species that do not meet any of the criteria in the vulnerable category. Nevertheless, some species that qualify as of least concern may not have been assessed against all the criteria because of a lack of relevant information. Such species could be listed as either least concern or DD. Often this depends on the judgment an assessor makes about the relevance of the assessed versus unassessed criteria.

The category near threatened is intended for species that only just fail to qualify as threatened. It is defined as a taxon that "has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for or is likely to qualify for a threatened category in the near future." The guidelines (IUCN 2006) do not specify criteria for near threatened, but suggest it is defined by how close a species is to meeting thresholds for the vulnerable criteria. Therefore, estimates of population size or habitat loss should be close to the vulnerable thresholds, especially if there is a high degree of uncertainty, or they should meet some of the subcriteria.

# Criteria for Critically Endangered, Endangered, and Vulnerable

#### CRITERION A: HIGH DECLINE RATE

For criterion A, an estimate of current population size is compared with an estimate from the past or a projection for the future, and the change over the specified time period t is compared with threshold values for critically endangered, endangered, and vulnerable (Fig. 3). Population size is adjusted with the measure of "mature individuals" (IUCN 2001), which is specifically defined to reflect the size of the actual or potential breeding population. Because mature individuals of different species have very different average life spans (from hours to millennia), the period over which declines are measured is expressed in generation lengths. Generation length acts as a surrogate for turnover rates within populations. Longlived species are at greater risk from increased annual adult mortality rates (measured as percentage of loss per year) than short-lived species because breeding adults experience this mortality over more years. Conversely, a long-lived species declining at the same rate as a shortlived one (measured as percentage of change per generation) shows smaller reductions over time (measured in years). The time window over which declines are measured is set to a minimum of 10 years because measuring changes over shorter time periods is difficult and does not reflect timescales for human interventions. The maximum projection into the future is 100 years, regardless of

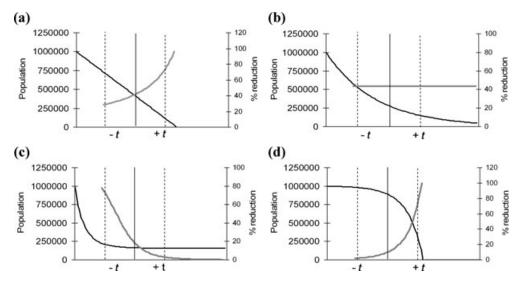


Figure 3. Different kinds of population decline used in criterion A. Each graph shows population size declining over time (black solid line) and the decline rate measured as number lost over the previous 10 years as a percentage of the starting number (gray solid line). The points in time marked —t and +t are the past and future points (dotted vertical lines), respectively, where assessment is made compared with the present (solid vertical line): (a) a constant number of individuals are lost in each time period; (b) a constant proportion are lost in each time period; (c) a declining proportion are lost in each time period; (d) an increasing number of individuals are lost in each time period.

generation time, because of the uncertainties in predicting population sizes a long way into the future as might be necessary for long-generation species.

The decline, measured as percentage of loss, can be estimated for the past (criterion A1 and A2), future (criterion A3), or a combination of the past and future (criterion A4). Because of difficulties in estimating population sizes in most natural populations, the criteria allow the assessor to use various kinds of direct and indirect evidence to estimate the decline rate, and the evidence is made explicit in the subcriteria. Criteria A1 and A2 listings may be derived from direct observation (population counts of some kind), which is obviously not feasible for future projections. For any of the criteria A1 through A4, declines may be determined on the basis of indices of abundance such as sightings or catch per unit effort. Assessment of rates of change in threatening processes may also be used for criterion A listings, on the basis of loss of habitat, levels of direct or indirect exploitation, and the effects of introduced taxa, hybridization, pathogens, pollutants, competitors, or parasites. Nevertheless, assessors need to use such indirect evidence cautiously. It is important to distinguish the decline in population size, with which we are concerned, from the underlying process. Harvesting, for example, is counteracted to some extent by density-dependent processes, such that the rate of decline is not linearly proportional to the number removed (Clark 1990). Similarly, a measured decline in habitat area cannot be straightforwardly translated to a decline in population size, especially if it involves losses of edges or lower-quality habitat (Lomolino & Channell 1995; Rodriguez 2002; Akçakaya et al. 2006).

Careful analysis of expected decline trajectories is needed because the shape of the decline-rate curve depends on the threat process involved (Fig. 3). Figure 3a shows a population declining by a constant amount each year such that the decline rate increases as the population becomes smaller. This might occur in a situation where interspecific competition, predation, or overexploitation leads to population reduction, but the reduction in population number is constant, perhaps related to the size of the predator or competitor population or the number of harvesting households. Here, past decline rates allow the species to qualify as vulnerable (decline >30%), but declines projected to continue on the same basis yield an endangered (>50%) categorization. If declines persist, this population will soon qualify for critically endangered (>80% decline) before going extinct.

Figure 3d shows the same process, but the depletion in population numbers is increasing over time. This situation is not unlikely, especially under habitat fragmentation and for species that provide consumer goods of high economic or social value where the value increases as the product becomes rarer or consumer tastes increase demand. Increased decline rates of smaller populations may be expected where inverse density dependence (known

as Allee effects or depensation) is operating (Myers et al. 1995; Courchamp et al. 1999; Courchamp et al. 2006). In this situation, the decline rate increases even more quickly with time; thus, in a very short time, the species moves from nonthreatened through the categories vulnerable, endangered, and critically endangered until it goes extinct. In such cases, as portrayed in Figs. 3a & 3d, it may be appropriate to derive a higher threat category by forward projection with criterion A3, rather than on the basis of current rates.

The trajectory in Fig. 3c shows a case where the population numbers decline over time, but the decline rate is decreasing. Given enough time, the population can stabilize and may even recover. The decline rate progressively decreases so that the species that originally qualified as critically endangered moves through the categories endangered and vulnerable until eventually it is not threatened. This pattern is expected under a variety of situations. For example, it could be the outcome of managed harvesting programs. Here managers may seek to reduce the population size until it reaches the density at which productivity is increased or maximized, and the harvest is then stabilized at a sustainable level, at which point there should be no further decline in population. Because the IUCN rules require listing under the category of highest threat, such species are listed according to past, not future, projected rates. Nevertheless, when there is confidence that the trend is declining, criterion A1 is used, rather than A2, and its more exclusive thresholds for listing allow the reduced extinction risk to be reflected (see later).

In Fig. 3b the decline rate is constant and the change in population size is reducing over time, perhaps as a function of the interaction between population change and density-dependent processes, for example, when the effects of exploitation, predation, or competition are reduced with the abundance of the species. The population in Fig. 3b always qualifies as vulnerable and will never qualify for any higher threat category under criterion A until it goes extinct. In practice, a species showing this pattern qualifies for higher threat categories under criteria B, C, and D once the population size or the geographic range reaches sufficiently low levels to meet the thresholds in these categories.

Criteria A1 and A2 differ according to whether or not the causes of decline are reversible, understood, and have ceased. Criterion A1 can only be used if all these conditions are met (IUCN 2006). If they are, the threshold decline rate is higher than in A2. Criterion A1 is likely to be used for species following trajectory 3c, where they are under good management and should have lower extinction risks than species with the same current decline rate but where future decline rates cannot be expected to be reduced.

The criteria do not specify how information on temporal changes in population size should be used to calculate

a past decline rate or project a future one. It may be appropriate to use some statistical method to calculate the decline rate, such as fitting a least-squares regression line and estimating the decline rate from the slope of the line. Nevertheless, it may often be inappropriate and impractical to do this. If populations show nonlinear trends within the 3-generation assessment period, such as when an increase in population is followed by a decrease, fitting such a regression line could be misleading. Also, for many species there are no systematic data on population size, and the assessor may need to make a determination of trends on the basis of extremely limited information. Often, the best that can be done is to use the estimated number at the beginning and end of the 3-generation census period. The potential problems in this approach are self-evident, but it is less obvious that even with apparently good information, it may be difficult to make a robust estimate of population trends. Accurate measurements of changes in population size depend critically on the quantity and quality of available data (Taylor 1995). Over limited time spans or with small numbers of surveys, it is possible either to fail to detect a real decline (Type II error) or to detect a decline when actually there is none (Type I error). Although statistical techniques such as power analysis can be used to support assessments (Taylor & Gerrodette 1993), they do not solve the problem if the situation is both extremely uncertain and potentially serious (Colyvan et al. 1999). In situations of uncertainty, the assessor should use the best available information and combine formal data analysis with expert judgment (Colyvan et al. 1999), for which methods are now available (Akçakaya et al. 2000).

#### CRITERION B: SMALL RANGE AREA AND DECLINE

Criterion B allows a species to qualify as threatened when its geographical range is very restricted and when other factors suggest that it is at risk. In some situations, population size may not be measurable or relevant to an elevated extinction risk, for example, when species are restricted to small areas or to habitat remnants that are themselves disappearing. Although this criterion was originally developed for plants, the drafting group considered this criterion applicable to other species, especially those at high densities within restricted areas or habitats.

This criterion does not simply use range area as a surrogate for population size. Although there is a very broad positive correlation within and across species between total geographic range size and population numbers, there is much variation and the details can alter according to the spatial scale at which the species is assessed (Gaston 1994a; Gaston et al. 2000; Blackburn et al. 2006). In some cases, species may qualify under population size and range size criteria, but more often the 2 measures will operate somewhat independently. Many species that qualify as threatened under criterion B can-

not qualify on the basis of population size. Conversely, some species (e.g., many marine mammals) cannot qualify under criterion B however close they are to extinction because the ranging patterns of individuals exceed the critical thresholds.

The measurement of range area is complicated (Gaston 1991; Gaston 1994a, 1994b, 1994c, 2003; Maurer 1994). The criteria consider 2 quantities, extent of occurrence (EOO) and area of occupancy (AOO) (sensu Gaston 1991). Extent of occurrence is defined as the area contained within the shortest continuous boundary that can be drawn to encompass all the known, inferred, or projected sites of occurrence of a species. This measure could be strongly influenced by cases of vagrancy and by marked discontinuities or disjunctions within the overall distribution of a species, both of which should be excluded. What constitutes a discontinuity or disjunction has deliberately been left vague, but of particular concern here are extents of occurrence composed of broad environments that are totally unsuitable for the species to occupy or often even to disperse into. For example, it would be inappropriate to include intervening areas of ocean when estimating EOO for a forest-dwelling species occurring at sites on 2 continents. The IUCN guidelines provide additional details on estimating EOO (IUCN 2006).

Area of occupancy quantifies the area within the EOO where the species is found. Species are hardly ever continuously distributed throughout their EOO. As applied in the criteria, AOO is the smallest area essential at any stage to the survival of existing populations of a species (e.g., colonial nesting sites, feeding sites for migratory species). The size of the AOO for a species inevitably depends on the spatial scale at which it is measured: the finer the resolution, the smaller the resultant area (Gaston 1991). There has been much debate over how this issue can best be resolved (Keith et al. 2000; Hartley & Kunin 2003).

Although no scale of measurement is specified in the criteria, the rules state that the scale should be appropriate to relevant biological aspects of the species and should be measured on a grid (or equivalents). The guidelines give more specific advice on avoiding problems of scale when using AOO (IUCN 2006). In general, spatial scales used for measuring ranges should reflect the movement and dispersal patterns of the species in question, and exceedingly fine or very coarse resolutions will lead to inappropriate listings under criterion B.

The measurement of EOO and AOO has been thought difficult for species with linear ranges (e.g., intertidal, stream, and riverine species). These range areas tend to be very small because one dimension (e.g., the width of the intertidal zone or the river) is so limited. In fact, species that depend on linear habitats are particularly vulnerable because a threat can rapidly affect an entire area (e.g., a single upstream pollution event may easily affect

a whole river downstream). On balance, therefore, areas of linear ranges are thought to provide a fair reflection of risk.

Unlike population decline rates and population sizes, there is no strong theoretical framework to associate given range areas (which may contain hugely different numbers of individuals) with different levels of risk of extinction. Therefore, although a range-area-based criterion was regarded as essential to the listing of many groups of organisms (for which population data are either not available or not of foremost importance in determining extinction risk), the choice of critical thresholds for criterion B has been plagued with difficulties from methodological and biological standpoints. The final decisions were made largely on an iterative basis of trial and error, and empirical testing by SSC experts using data on a variety of relevant species. This resulted in the maintenance of a constant ratio of cut-off values for EOO and AOO (a difference of a factor of 10) in each of the categories critically endangered, endangered, and vulnerable and cut-offs, respectively, of 100 km<sup>2</sup>, 5,000 km<sup>2</sup>, and 20,000 km<sup>2</sup>. All these areas, for EOO and AOO, are comparatively small, reflecting that for this criterion, risk of extinction is associated with range area itself.

Unless extremely small (see criterion D), limited range size is not sufficient on its own for a species to qualify as threatened. Many species have persisted successfully for long periods within small global ranges and have a low risk of extinction (Gaston 1994a; Gaston 2003). To qualify under criterion B, therefore, a species must also exhibit at least 2 of 3 other symptoms of risk. To avoid overlisting, the conditions were made difficult to meet. There must be some evidence the population is or is projected to be in continuing decline, severely fragmented, limited to a few locations, or subject to extreme fluctuations. Empirical and theoretical studies suggest that all these conditions will increase the likelihood of extinction.

Commentary on criterion B suggests that it may be overly inclusive, with the threshold values set so high that a large number of species are inappropriately listed as threatened (Keith 1998). In fact, for certain small natural areas, such as oceanic islands, where the total area under analysis is small, there is little habitat heterogeneity, and threats are pervasive, all endemic species may justifiably qualify as threatened. Nevertheless, species cannot be listed as threatened solely on the basis of small range areas, so the number of such cases is limited. More often the area under assessment is small because it is a politically defined subunit within a wider area, in which case the assessment should include the status of the species outside the area (IUCN 2003). Similarly, it has been suggested that the different criteria should give similar threat assessments across species and that the numbers listed in the categories of threat should be evenly spread (Keith 1998). Nevertheless, we see no reason a priori why either of these should follow because the criteria are intended to operate independently of one another and threats are expected to vary between species and habitats.

#### CRITERION C: SMALL POPULATION SIZE AND DECLINE

Criterion C focuses on populations that are numerically small and in continuing decline and is the most straightforward of all to place in a theoretical framework. The choice of threshold sizes for the number of mature individuals is derived from theoretical values for minimum viable populations (see above) adjusted to reflect timescales appropriate for the species. The initial condition is that the population must number fewer than 10,000 mature individuals (for vulnerable), 2,500 mature individuals (for endangered), and 250 individuals (for critically endangered). The steep ramping down of critical population sizes reflects what is known from theoretical studies about the general relationships between population size and time to extinction under various kinds of environmental and demographic stochasticity (Lande 1993, 1998).

A population in continuing decline may immediately qualify if the population size meets the threshold values above and the population is declining sufficiently fast (criterion C1). If a decline is known or expected, but is not measurable or sufficiently severe to meet the C1 threshold, the species may qualify instead under C2. For this to happen, its population must exist entirely or almost as a single unit, have relatively small subpopulations, or experience extreme fluctuations in size. Species cannot qualify for criterion C simply by meeting the population size threshold and being in decline. The additional conditions are more difficult to meet in criterion B than in criterion C because there is direct evidence in C that the population size is already small, which is not necessarily the case in B. Therefore, although criteria B and C are comparable, the difference between range areas and population sizes as entry points to the criteria mean that the subcriteria and conditions should not be the same in each (Keith 1998).

#### CRITERION D: VERY SMALL POPULATION SIZE

Criterion D allows species to be listed as threatened without evidence that there has been, is, or will be a decline of some sort. It was developed because theoretical models show that numerically small populations can have relatively high extinction risks solely from internal processes. The term *demographic stochasticity* has been used to describe the process whereby random variation among individuals in demographic vital rates or random variation in sex ratio alone can lead to population extinction (Goodman 1987; Lande 1993), the importance of which is supported empirically by a number of studies on very restricted populations (Kokko & Ebenhard 1996; Legendre

et al. 1999). Although demographic stochasticity is generally unimportant for populations with effective population sizes over about 100 individuals, its deleterious effects are amplified by life history and behavioral differences among species (Sorci et al. 1998; Legendre et al. 1999). Hence, the threshold numbers used in the criteria are larger. For vulnerable, this means any species with fewer than 1000 mature individuals can qualify. The equivalent figures for endangered and critically endangered are 250 and 50. The scaling of these values reflects the relationship between population size and extinction time (Fig. 1).

Criterion D has a subcriterion D2 that is present only in the vulnerable category. Subcriterion D2 allows species to qualify solely on the basis of a very restricted distribution (i.e., it is the range-area equivalent of D1). Subcriterion D2 is conceptually distinct, however, because it is implicit in its definition that it is not restricted range alone that should be used to list species under this category. Rather, it is evidence that the species is actually threatened because of its very restricted distribution. The D2 subcriterion has sometimes been misused, mainly through applying the numerical thresholds mentioned in the first part of the definition without reference to the second part. Summary tables of the criteria, increasingly used by assessors instead of the full text, tend only to include the numerical guidelines, and this may have increased the extent of misinterpretation.

Subcriterion D2 does not extend into the higher-risk categories because the justifications for listing are even more problematic at higher levels of risk. Although D2 is justified under the precautionary principle at the relatively low levels of risk embraced by vulnerable, this is not so for endangered and critically endangered. Some users believe D2 should be extended to allow listings higher than vulnerable for extremely restricted species (Seddon 1998), whereas others find D2 overly inclusive and are critical that it apparently fails to recognize that for many species rarity is a natural state and only certain kinds of rare species are actually liable to go extinct (de Lange & Norton 1998). During the criteria review, the conditions for D2 were tightened to avoid overlisting, but it remains among the most inconsistently applied elements of the IUCN criteria.

#### CRITERION E: UNFAVORABLE QUANTITATIVE ANALYSIS

Criterion E allows the assessor to use any kind of quantitative analysis for assessing the risk of extinction, which is then compared with the extinction-risk thresholds given for each of the categories. These quantitative thresholds are expressed as the probability of extinction within a given time frame. The time frame is measured in years or generations as in the formulation of criterion A, with whichever of the 2 is longer. Justifications for the thresholds are essentially the same as in Mace and Lande (1991),

except that the time frame for critically endangered has changed from 5 to 10 years, for consistency with the other criteria, and the future time frame is capped to 100 years as in criterion A.

The term quantitative analysis was chosen carefully to avoid the impression that this criterion necessarily involves a population viability analysis (PVA). Criterion E can be used in any case where a robust estimate of extinction risk can be derived. Often this might be done without detailed information on population dynamics and is derived from information on the status of the habitat. For example, consider the situation in which a species is endemic to an area and is forest dependent and forestry rights have been sold to allow the entire area within which this species lives to be cleared within 20 years. Such a species would certainly qualify as endangered and even possibly as critically endangered because there is at least a 50% chance that the critical habitat areas will be cleared in the first 10 years. Many similar cases in which criterion E can be used involve land-use changes and expected levels of exploitation. It can also be used if there is a high risk of invasion by a species whose presence would be disastrous for the resident species.

More commonly, however, a PVA would be involved in the assessment. The rules dictate that the structure of the model and the data used in the analysis be made explicit, and standards have been developed (IUCN 2001, 2006). There are several potential difficulties with widespread use of PVA modeling in red list assessments. First, despite the requirements that the assumptions be made explicit, it is in practice difficult to list and justify the background to a PVA analysis without lengthy documentation. Listings under criterion E would thus require longer justification than listings under other criteria.

Second, PVA outcomes can be very sensitive to the levels of some input variables. For example, expected changes in habitat availability, the incidence and severity of catastrophes, levels of mortality, and the interaction between population size and inbreeding depression might each determine the extinction risk category on their own when set to plausible, although improbable, values in a PVA model. It will be hard for IUCN to monitor and guarantee standards when accuracy depends on validating many such sensitive variables (Mangel & Tier 1994; Ludwig 1996, 1999).

Conversely, PVA models may not be precautionary in the absence of good information if they assume favorable values for key parameters (e.g., Armbruster et al. 1999). Although carefully constructed PVAs built on reliable data can apparently predict risks of decline accurately (Brook et al. 2000), many practitioners suggest that PVA is best used as a way of assessing the relative risks of different processes or the relative benefits of different management strategies, but not the absolute risk of extinction (Akçakaya & Burgman 1995; Beissinger & Westphal 1998). We concur with this view and recommend

use of criterion E for simple and explicit modeling on the basis of reliable and sufficient data, rather than on the basis of outcome of detailed models with uncertain parameters and a large number of assumptions.

### **Key Issues and Their Resolution**

Throughout the period of drafting, consultation, and redrafting of the criteria, several features of the system were continuously debated and have arisen repeatedly in discussions since the system was adopted. Below we review some of these features and explain the nature of the debates and their eventual resolution.

#### **Assessing Threats versus Setting Priorities**

There is an important difference between measuring threats and assessing conservation priorities. The IUCN system classifies species according to their risk of extinction and is not on its own sufficient to determine priorities for conservation. Priorities for conservation actions may include numerous other factors such as costs, benefits, logistics, chances of success, and other biological characteristics of species and communities (Mace et al. 2007). Nevertheless, assessing taxa with the IUCN Red List Criteria is often a critical first step in setting priorities for conservation action. One important motivation behind the development of the red list categories was the need to identify those species at highest risk of extinction, for which it was urgent to assess their situation, and to design and implement effective conservation actions. The IUCN Red List is best used as a means to identify urgent cases, rather than as a simple priority-setting tool.

#### The Red List Categories and Conservation Actions

Many taxa assessed under the IUCN Red List criteria will already be subject to conservation actions, and the system is designed so that the criteria are applied to a species whatever the level of conservation action it is under. A species may require conservation action even if it is not listed as threatened, and effectively conserved threatened taxa may, as their status improves over time, cease to qualify for listing.

In certain cases, conservation actions alone may be responsible for preventing a species slipping from unthreatened into the threatened categories. There is therefore the possibility that effective conservation of a threatened species could lead to downlisting and have the unintended consequence of reducing justification for conservation actions, thereby contributing to increased threat. In earlier versions of the criteria, a subcategory outside the threatened categories (conservation dependent) was available to denote such cases (IUCN 1994). Because this is not a measure of extinction risk status, the relationship of this category to the overall scheme was unclear, and

the category was removed in version 3.1 (IUCN 2001). Nevertheless, it is recommended that such cases be listed in Near Threatened (IUCN 2006) with appropriate documentation.

#### **Global versus National Listing**

The IUCN Red List assesses the status of species at global level because this is the scale at which extinction occurs. Although local extinction (or extirpation) is often of great concern, a species is not extinct while it remains extant somewhere else. Although the relationship between subglobal to global extinction is clear, the relationship of global to regional threatened status is unfortunately much more complicated (Gärdenfors 1996; Gärdenfors et al. 2001). Certain species may be assessed to be relatively secure within a country but nevertheless be at risk globally, whereas other species that are relatively secure globally may be highly threatened within a particular region, for example, at the edge of their geographic range. Although red list assessments make most sense at the global scale or at least at large spatial scales, effective conservation actions generally take place nationally and locally. Indeed, few mechanisms are available to conserve species above the national level, and global conservation agreements such as CITES and the Convention on Biological Diversity (CBD) recognize national sovereignty and rely primarily on implementation within countries.

The methods used for national and regional conservation assessments are therefore of great significance for species conservation. It is becoming increasingly common for countries to compile national red lists that identify species at high risk nationally, and they often base their lists on the IUCN system (Miller et al. 2006, 2007). Continuing work is underway to improve the consistency between the data and assessment methods used nationally and globally, but extinction risk within restricted political areas is a complex concept because of the interdependence of many species on adjoining political units, and there will inevitably be variability among countries in assessment methods and uses of these lists (Rodriguez et al. 2004; Eaton et al. 2005; Samways 2006; Miller et al. 2007).

#### Accuracy, Precision, and Extinction Prediction

Increasingly, the conservation status of species features in disputes that are significant politically and economically, so the system on which listings are based comes under close scrutiny and perhaps even legal challenge. Wider use of data in the IUCN Red List has also affected funding opportunities for regions, countries, and nongovernmental organizations. Such circumstances make it essential that IUCN be able to demonstrate scientific independence and rigor in the listing process. Nevertheless, moving from qualitative to quantitative criteria has produced the unexpected outcome that listings are

both more likely to be challenged, and harder to support. The system is not intended to provide robust predictions about the fate of individual species; this would require a species-specific assessment often with improved data and a carefully designed or selected model. Many misuses of IUCN Red List classifications derive from the misconception that each category corresponds to a specific extinction risk, and that it indicates protection or conservation actions must necessarily follow.

The IUCN system is a probabilistic assessment of the likelihood that a species in a particular threat category will go extinct within some stated time frame, and it cannot be used to provide a robust prediction about the fate of a particular species. Instead the classification is expected to lead to accurate categorizations of species in that (in the absence of conservation interventions) a larger proportion of species listed in higher threat categories will go extinct over shorter periods. We anticipate that these proportions and periods correspond roughly with the values given for each category in criterion E, but this cannot be proven. In addition, the extinction risk expressed in criterion E cannot be applied to a species that qualifies on the basis of any of the other criteria within a category.

Because the system is probabilistic, it is inevitable that certain species will be listed as at risk yet do not actually go extinct. Moreover, the system is precautionary, and in any risk-averse system, it is inevitable there will be some overlisting. The act of listing species on a red list should lead to increased conservation, protection, and conservation success (Butchart et al. 2006b), the list thereby becomes a self-denying prophecy. The intention is to minimize the number of species falsely listed as threatened, but this cannot be achieved without excluding some that should be listed. Drawing this line is difficult, but for all the reasons stated earlier, the number of species listed should not be used to predict future extinction risks for a single species or to predict extinction rates for entire groups.

It has been indicated repeatedly, including herein, that a threatened categorization does not necessarily indicate conservation actions are required. Instead listing in one of the threat categories indicates that attention to the species is necessary and urgent, and that relevant bodies and agencies, often with more detailed information at hand, must soon undertake a diagnosis and design and implement appropriate conservation actions.

#### Listings Determined on the Basis of Decline Rates Only and the Status of Large Populations

On the basis of decline rates only and with no threshold population sizes, criterion A has the potential to force the inclusion of some extremely abundant populations onto lists of threatened species. Criterion A has therefore been controversial, especially for widespread species with historical declines that are believed to have stabilized (Webb & Carrillo 2000; Broderick et al. 2006; Godfrey & Godley, 2008) and for fisheries species (Matsuda et al. 1997; Matsuda et al. 1998; Mace & Hudson 1999; Musick 1999; Hutchings 2001). One suggestion is that the accuracy of criterion A be improved by factoring in resilience (Musick 1999), but there is little evidence that high fecundity or resilience influences extinction risk in marine fishes (Dulvy et al. 2005; Reynolds et al. 2005). In addition, recent recommendations to improve the assessment of extinction risk in marine fishes (Hutchings & Reynolds 2004; Cheung et al. 2005; Reynolds et al. 2005) are concordant with, although clearly more detailed than, the IUCN system.

The justification for criterion A is evident from decline processes such as those illustrated in Figs. 3a & 3d, where constant or increasing population decline leads rapidly to loss of population numbers. Recent examples of this include the massive decline of vultures in the Indian subcontinent as a result of inadvertent poisoning and the decline of the Tasmanian devil (Sarcopbilus barrisii) due to disease (Prakash et al. 2003; McCallum 2007). Nevertheless, patterns such as those in 3b and 3c illustrate the not uncommon cases where decline rates decrease over time and threatened listings only last until the decline rate drops below the threshold value. The array of plausible patterns of decline and the requirement to apply the criteria in a precautionary manner mean that the choice of threshold values is a difficult balance between levels that detect species in decline well before they reach critically low levels and levels that falsely list species nearing the end of a decline that is slowing and will soon cease. These thresholds were repeatedly tested and reviewed during the development of the criteria, and the levels chosen are the best compromise that could be found.

Undoubtedly criterion A is important, but species listed in this way can represent a wide array of circumstances. In the case of species listed only under criterion A, and especially those at the highest risk, there is real urgency to assess the causes of the decline and determine what interventions (if any) are necessary.

#### **Rarity and Stochastic Threats**

The most fundamental intended use of the system is to measure extinction risk and not other factors, such as rarity, ecological role, or economic importance, which are commonly incorporated into systems that establish conservation priority (Munton 1987; de Grammont & Cuaron 2006). Consequently, trends in abundance and range size are generally more important for listing species than are single measures of absolute population size or areas of distribution. Nevertheless, there are various kinds of extinction processes, ranging from the highly predictable and deterministic (such as wholesale habitat clearance) to the unpredictable and stochastic (such as invasions,

epidemics, or political changes). Populations that are not declining, but are restricted in size or range may be vulnerable to large-scale or unpredictable threats despite their current stable status.

This situation has led to an ongoing debate that concerns the listing of small and stable versus large but declining populations. In earlier versions, the category susceptible was included (Mace et al. 1992). This was distinct from the other threatened categories, but could be used to list species that were rare (very limited in population size or very restricted in area) and were thus always potentially vulnerable to extinction, even though there was no apparent trend or threat. The debate over the susceptible category revolves around the fact that many species are naturally rare (Gaston 1994b; de Lange & Norton 1998; Hartley & Kunin 2003) and possess lifehistory characters that allow them to persist in this state (although rarity itself is obviously not an evolved trait: Kunin & Gaston 1993). Yet these very restricted forms are undoubtedly more vulnerable than are more abundant and widespread species. A category or criterion for rare species has the effect of greatly increasing the number of species listed and inevitably results in the inclusion of many that are unlikely to go extinct within ecological time frames. Nevertheless, without such a category or criterion, many species thought to be key to the overall preservation of biodiversity are listed alongside the most abundant and widespread forms as of least concern.

Opinion on how to deal with these species changed several times throughout the drafting process. The final verdict was to allow a rather restrictive subcriterion for rare species (criterion D2) under vulnerable only (not in the more threatened categories) and to place it in one of the existing criteria (criterion D). Nevertheless, as discussed earlier, D2 is defined vaguely and is perceived to be applied inconsistently in practice.

#### **Common Criteria for All Species**

A difficult issue was how to ensure that all species, despite their wide variation in life history and ecology, would be assessed equitably. The early decision to focus on a single set of criteria for all species was a recognition that life history, rather than taxonomic affiliation, was the appropriate way to classify species for assessment. This meant that species with different life histories should enter evaluation with comparable sets of parameter estimates. Rather than have the criteria for the threatened categories become long and complicated, a few parameters were chosen and carefully defined so that very different kinds of species could be compared. In particular, "generation length" is a scalar for all time-dependent measures, and "mature individuals" is used throughout the criteria in place of any measure of overall population size.

The concern is still often expressed that the same criteria cannot be applied to all species. To the contrary, we believe the approach taken is biologically and operationally the most reasonable, but we acknowledge its effective operation depends critically on transforming the traits and data from different species into comparable and relevant values to test against the criteria. This should be achieved by the definition of key terms that form an integral part of the criteria and by the rules for their use. These definitions have unfortunately received much less critical external review than have the numerical thresholds in the criteria, although we believe they are often more significant.

#### **Uncertainty**

The rules for application of the criteria (IUCN 2001) make it clear that precise data are not required and that the assessor can use expert knowledge along with the best information available to make estimates about current or future trends, for which detailed guidance is given (IUCN 2001, 2006). Nevertheless, it is unclear whether this advice is followed in practice, even though techniques for dealing with uncertainty in the IUCN classification have improved over time (Todd & Burgman 1998; Colyvan et al. 1999; Akçakaya et al. 2000). There is now software available to use these new methods (IUCN 2006; Akçakaya & Root 2007) that we believe is an important means to standardize and make explicit the way in which uncertainty has been handled.

The criteria (IUCN 2001; Annex 1) and the guidelines (IUCN 2006) recommend representing uncertainty by assigning species to a range of categories, instead of a single category. This range of plausible categories (Akçakaya et al. 2000) is derived by representing each variable used in an assessment (e.g., decline rate, population size, EOO, AOO) as a best estimate and a plausible range. Because the criteria require each species to be assigned to a single category, the range of categories representing uncertainty is indicated only in the documentation of the listing. An important point emphasized in the criteria and the guidelines is that when the variables are uncertain, the reduction of the uncertainty into a single category of threat involves attitudes to risk and uncertainty (e.g., risk tolerance, ranging from precautionary to evidentiary [see later]). Thus, even though there will always be subjectivity when dealing with cases with large amounts of uncertainty, the recommended methods make such attitudes transparent and provide an objective way of transforming data uncertainties into a range of plausible threat categories.

# **Data Deficiency and Appropriate Categorization**

The DD category is used for species for which there is insufficient information to determine a threat category. It is not the amount of information that is important here so

much as whether or not the available information is relevant. Sometimes species can be reliably classified against the criteria on the basis of very little information. Clear evidence of decline, for example, will often be sufficient even in the absence of any population data, and sometimes habitat maps and some knowledge of the species' ecology is enough to determine that it cannot meet any of the threshold values and should therefore be listed as least concern. Nevertheless, it is still the case that a relatively large number of evaluated species may best be coded as DD.

The decision as to the adequacy of information depends on attitudes to risk and uncertainty (Akçakaya et al. 2000). For example, an extreme precautionary stance implies a species should be listed as threatened until it meets none of the criteria. An extremely evidentiary (risk-prone) approach dictates that all species be assumed secure until evidence suggests they really are at risk. Species that do not meet any of the criteria are then listed as least concern. The criteria rules suggest adoption of a position that tends slightly toward the precautionary standpoint. Therefore, meeting any one criterion necessarily qualifies a species as threatened, but not meeting several criteria may lead to listing as either least concern or DD.

#### **Depleted Species**

Because the criteria are designed to detect species at risk of extinction, they do not identify species that were once much more numerous. Once a species is at a level above the threshold values on criteria B and C and the decline is a historical event, the species drops off the threatened list. Many species now inhabit only fragments of what was once their geographical range, and it is regrettable that it is so easy to forget this (Gaston & Fuller 2007; Gaston & Fuller 2008). The continuous downgrading of our conservation objectives in line with this shifting baseline is, of course, undesirable (Balmford 1999), so it is important to recognize that the criteria do not reflect the general status of biodiversity within a full historical context. Their focus on measuring risk of extinction means that continuing to list species that are still numerous and stable, such as the species depicted in Fig. 4, cannot be justified. Although many people would like to see some explicit notation for depleted species, it is important to keep these 2 issues separate. Another issue concerns the slow but persistent depletion of common species, which may often be insufficient to trigger listing until the population reaches critically low levels. Nevertheless, the purpose of the IUCN Red List is to identify species at risk of global extinction, so there is no basis for including these species during this period of decline.

#### **Conclusions**

The development of quantitative criteria for the IUCN Red List began nearly 20 years ago because of the emerg-

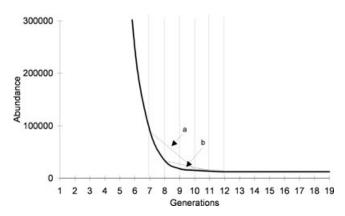


Figure 4. Assessment of depleted species by the International Union for the Conservation of Nature (IUCN) criteria. The graph depicts a hypothetical species that has gone through a period of rapid decline but has now stabilized at a new, much-reduced level. The new population size is above 10,000 mature individuals, which means by the 12th generation the species does not qualify for listing under IUCN criteria B or C, although it does qualify under criterion A. The species qualifies as critically endangered until generation 10 (decline rate indicated by line a) and then drops down through the threat categories until generation 12, at which point the decline rate drops below the threshold value for vulnerable (decline rate indicated by line b). Thereafter, the species no longer qualifies as threatened.

ing need to bring rigor and objectivity into the world's only officially recognized list of threatened species. This process has identified and stimulated debates over emerging scientific issues and confronted many practical difficulties in applying and interpreting the resulting assessments. The consequences of developing the new criteria have been far broader and deeper than could have been anticipated in the 1980s. Apart from its many uses in species conservation, the IUCN Red List is used in applied and theoretical conservation research, in legislation, and for national and international conservation planning and priority setting. Uptake of the IUCN Red List criteria has also been extensive at national level; at last count 76 countries were using them.

The IUCN Red List is also now one of the bases for internationally agreed indicators to monitor the status of global biodiversity (see www.twentyten.net). The Red List Index (RLI) has been developed as a method to track the movement of species through the red list categories over time and can be used to assess the rate at which threatened species are moving toward extinction (Butchart et al. 2004, 2007). Initially developed around comprehensively assessed groups, such as birds, amphibians, and mammals, the RLI has been extended to measure the status of a representative set of all species by stratified sampling within major taxa (Baillie et al. 2008).

The RLI has been adopted as one of the indicators for the Convention on Biological Diversity's 2010 target (Mace & Baillie 2007).

Given the extent to which the system and species classifications derived from it are embedded in national and international biodiversity legislation and monitoring systems, adjustments to the system and to the criteria could have a number of unforeseen consequences. Although the system may be far from perfect, we suggest that it is sufficient for its purpose and that any further adjustments requested or made could undermine its many longer-term benefits, including that of a global index of change in biodiversity status.

# Acknowledgments

We are grateful to many people who contributed to this work over many years of development and implementation. In particular, we thank M. Avery, J. Baillie, M. Burgman, S. Butchart, J. Cooke, J. Ginsberg, D. Keith, R. Lande, M. Maunder, M. Seddon, and A. Stattersfield. We are grateful to J. P. Rodríguez, U. Gärdenfors, and 2 anonymous referees for helpful comments and suggestions. G.M.M. received funding from the NERC and the Pew Charitable Trusts. K.J.G. holds a Royal Society-Wolfson Research Merit Award.

#### Literature Cited

- Akçakaya, H. R., and M. Burgman. 1995. PVA in theory and practice. Conservation Biology 9:705-707.
- Akçakaya, H. R., and W. T. Root. 2007. RAMAS red list: spatial and temporal data analysis for threatened species classifications under uncertainty (version 3.0 Professional). Applied Biomathematics, Setauket, New York.
- Akçakaya, H. R., S. Ferson, M. A. Burgman, D. A. Keith, G. M. Mace, and C. R. Todd. 2000. Making consistent IUCN classifications under uncertainty. Conservation Biology 14:1001–1013.
- Akçakaya, H. R., S. H. M. Butchart, G. M. Mace, S. N. Stuart, and C. Hilton-Taylor. 2006. Use and misuse of the IUCN Red List criteria in projecting climate change impacts on biodiversity. Global Change Biology 12:2037–2043.
- Armbruster, P., P. Fernando, and R. Lande. 1999. Time frames for population viability analysis of species with long generations: an example with Asian elephants. Animal Conservation 2:69-73.
- Baillie, J. E. M., C. Hilton-Taylor, and S. N. Stuart (editors). 2004. A global species assessment. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- Baillie, J. E. M., B. Collen, R. Amin, H. R. A. Akçakaya, S. H. M. Butchart, N. Brummitt, T. R. Meagher, M. Ram, C. Hilton-Taylor, and G. M. Mace. 2008. Towards monitoring global biodiversity. Conservation Letters DOI: 10.1111/j.1755-263X.2008.00009.x.
- Balmford, A. 1996. Extinction filters and current resilience: the significance of past selection pressures for conservation biology. Trends in Ecology & Evolution 11:193–196.
- Balmford, A. 1999. (Less and less) Great expectations. Oryx 33:87–88.
  Beddington, J. R., and R. M. May. 1977. Harvesting populations in a randomly fluctuating environment. Science 197:463–465.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821-841.

Blackburn, T. M., P. Cassey, and K. J. Gaston. 2006. Variations on a theme: sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. Journal of Animal Ecology 75:1426-1439.

- Broderick, A. C., R. Frauenstein, F. Glen, G. C. Hays, A. L. Jackson, T. Pelembe, G. D. Ruxton, and B. J. Godley. 2006. Are green turtles globally endangered? Global Ecology and Biogeography 15:21–26.
- Brook, B. W., J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akçakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387.
- Butchart, S. H. M., A. J. Stattersfield, L. A. Bennun, S. M. Shutes, H. R. Akçakaya, J. E. M. Baillie, S. N. Stuart, C. Hilton-Taylor, and G. M. Mace. 2004. Measuring global trends in the status of biodiversity: Red list Indices for birds. Public Library of Science Biology 2:e383.
- Butchart, S. H. M., A. J. Stattersfield, and T. M. Brooks. 2006a. Going or gone: defining 'Possibly Extinct' species to give a truer picture of recent extinctions. Bulletin of the British Ornithologists' Club 126a:7-24.
- Butchart, S. H. M., A. J. Stattersfield, and N. J. Collar. 2006b. How many bird extinctions have we prevented? Oryx 40:266–278.
- Butchart, S. H., et al. 2007. Improvements to the red list index. Public Library of Science One **2(1):**e140.
- Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215-244.
- Cheung, W. W. L., T. J. Pitcher, and D. Pauly. 2005. A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. Biological Conservation 124:97–111.
- Clark, C. W. 1990. Mathematical bioeconomics. Wiley Interscience, New York.
- Collar, N. 1996. The reasons for red data books. Oryx 30:121-130.
- Collar, N. J. 1998. Extinction by assumption; or, the Romeo error on Cebu. Oryx 32:239–244.
- Collar, N. J., M. J. Crosby, and A. J. Stattersfield. 1994. Birds to watch 2 the world list of threatened birds. BirdLife International, Cambridge, United Kingdom.
- Colyvan, M., M. A. Burgman, C. R. Todd, H. R. Akçakaya, and C. Boek. 1999. The treatment of uncertainty and the structure of the IUCN threatened species categories. Biological Conservation **89**:245–249.
- Coulson, T., G. M. Mace, E. Hudson, and H. Possingham. 2001. The use and abuse of population viability analysis. Trends in Ecology & Evolution 16:219–221.
- Courchamp, F., E. Angulo, P. Rivalan, R. J. Hall, L. Signoret, L. Bull, and Y. Meinard. 2006. Rarity value and species extinction: the anthropogenic Allee effect. Public Library of Science Biology 4:2405–2410.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. Trends in Ecology & Evolution 14:405-410.
- de Grammont, P. C., and A. D. Cuaron. 2006. An evaluation of threatened species categorization systems used on the American continent. Conservation Biology 20:14–27.
- de Lange, P. J., and D. A. Norton. 1998. Revisiting rarity: a botanical perspective on the meanings of rarity and the classification of New Zealand's uncommon plants. Royal Society of New Zealand Miscellaneous Series 48:145-160.
- Diamond, J. M. 1984. "Normal" extinctions of isolated populations. Pages 191–246 in M. H. Nitecki, editor. Extinctions. University of Chicago Press, Chicago.
- Dulvy, N. K., S. Jennings, N. B. Goodwin, A. Grant, and J. D. Reynolds. 2005. Comparison of threat and exploitation status in North-East Atlantic marine populations. Journal of Applied Ecology 42:883– 891.
- Eaton, M. A., R. D. Gregory, D. G. Noble, J. A. Robinson, J. Hughes, D. Procter, A. F. Brown, and D. W. Gibbons. 2005. Regional IUCN red listing: the process as applied to birds in the United Kingdom. Conservation Biology 19:1557–1570.
- Fisher, D. O., and I. P. F. Owens. 2004. The comparative method in conservation biology. Trends in Ecology & Evolution 19:391–398.

Fitter, R., and M. Fitter, editors. 1987. The road to extinction. International Union for the Conservation of Nature, Gland, Switzerland.

- Foufopoulos, J., and A. R. Ives. 1999. Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. The American Naturalist 153:1-25.
- Frankham, R. 1995*a*. Conservation genetics. Annual Review of Genetics **29:**305–327.
- Frankham, R. 1995b. Effective population-size adult-population size ratios in wildlife—a review. Genetical Research 66:95–107.
- Frankham, R. 1999. Quantitative genetics in conservation biology. Genetical Research 74:237–244.
- Gärdenfors, U. 1996. Application of IUCN Red List categories on a regional scale. Pages 63-66 in J. Baillie and B. Groombridge, editors. The 1996 IUCN Red List of threatened animals. IUCN, Gland, Switzerland.
- Gärdenfors, U. 2001. Classifying threatened species at national versus global levels. Trends in Ecology & Evolution 16:511-516.
- Gärdenfors, U., J. P. Rodríguez, C. Hilton-Taylor, C. Hyslop, G. M. Mace, S. Molur, and S. Poss. 1999. Draft guidelines for the application of IUCN Red List criteria at regional and national levels. Species 31/32:58-70.
- Gärdenfors, U., C. Hilton-Taylor, G. M. Mace, and J. P. Rodríguez. 2001. The application of IUCN Red List criteria at regional levels. Conservation Biology 15:1206–1212.
- Gaston, K. J. 1991. How large is a species' geographic range? Oikos 61:434-438.
- Gaston, K. J. 1994a. Measuring geographic range sizes. Ecography 17:198-205.
- Gaston, K. J. 1994b. Rarity. Chapman & Hall, London.
- Gaston, K. J. 1994c. Spatial covariance in the species richness of higher taxa. Pages 221–242 in M. E. Hochberg, J. Clobert, and R. Barbault, editors. Aspects of the genesis and maintenance of biological diversity. Oxford University Press, Oxford, United Kingdom.
- Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, United Kingdom.
- Gaston, K. J., and R. A. Fuller. 2007. Biodiversity and extinction: losing the common and the widespread. Progress in Physical Geography 31:213-225.
- Gaston, K. J., and R. A. Fuller. 2008. Commonness, population depletion, and conservation biology. Trends in Ecology & Evolution 23:14-19
- Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance-occupancy relationships. Journal of Applied Ecology 37(supplement 1):39–59.
- Godfrey, M. H., and B. J. Godley. 2008. As we see it: seeing past the red—flawed IUCN global listings for sea turtles. Endangered Species Research. DOI:10.3354/esr00071 (available at http://www.int-res.com/articles/esr2008/theme/IUCN/IUCNpp2.pdf).
- Goodman, D. 1987. The demography of chance extinction. Pages 11-34 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, United Kingdom.
- Green, A. J. 1996. Analyses of globally threatened Anatidae in relation to threats, distribution, migration patterns, and habitat use. Conservation Biology 10:1435–1445.
- Harcourt, A. H. 1995. Population viability estimates: theory and practice for a wild gorilla population. Conservation Biology 9:134-142.
- Harcourt, A. H., and S. A. Parks. 2003. Threatened primates experience high human densities: adding an index of threat to the IUCN Red List criteria. Biological Conservation 109:137-149.
- Hartley, S., and W. E. Kunin. 2003. Scale dependency of rarity, extinction risk, and conservation priority. Conservation Biology 17:1559-1570.
- Hedrick, P. W. 1992. Genetic conservation in captive populations and endangered species. Pages 45-68 in S. K. Jain and L. W. Botsford, editors. Applied population biology. Kluwer Academic, Dordrecht, The Netherlands.
- Hudson, E., and G. M. Mace. 1996. Marine fish and the IUCN Red List of threatened animals. Zoological Society of London, London.

Hutchings, J. A. 2001. Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. Canadian Journal of Fisheries and Aquatic Sciences 58:108–121.

- Hutchings, J. A., and J. D. Reynolds. 2004. Marine fish population collapses: consequences for recovery and extinction risk. BioScience 54:297–309.
- Isaac, N. J. B., and G. Cowlishaw. 2004. How species respond to multiple extinction threats. Proceedings of the Royal Society of London B 271:1471-2954.
- IUCN. 1993. Draft IUCN Red List categories. IUCN, Gland, Switzerland.IUCN. 1994. IUCN Red List categories. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- IUCN. 1996. The 1996 IUCN Red List of threatened animals. J. Baillie and B. Groombridge, editors. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- IUCN. 2001. IUCN Red List categories and criteria: version 3.1. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- IUCN. 2002. IUCN Red List of threatened species. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- IUCN. 2003. Guidelines for application of IUCN Red List criteria at regional levels: version 3.0. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- IUCN. 2006. Guidelines for using the IUCN Red List Categories and Criteria. Version 6.2. Prepared by the Standards and Petitions Working Group of the IUCN SSC Biodiversity Assessments Sub-Committee. IUCN, Gland, Switzerland. Available from http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf (accessed January 2008).
- IUCN, Conservation International, and NatureServe. 2006. Global amphibian assessment. IUCN, Washington, D.C. Available from www.globalamphibians.org (accessed August 2008).
- Keith, D. A. 1998. An evaluation and modification of World Conservation Union Red List criteria for classification of extinction risk in vascular plants. Conservation Biology 12:1076-1090.
- Keith, D. A., T. D. Auld, M. K. J. Ooi, and B. D. E. Mackenzie. 2000. Sensitivity analyses of decision rules in World Conservation Union (IUCN) Red List criteria using Australian plants. Biological Conservation 94:311-319.
- Kokko, H., and T. Ebenhard. 1996. Measuring the strength of demographic stochasticity. Journal of Theoretical Biology 183:169-178.
- Kunin, W. E., and K. J. Gaston. 1993. The biology of rarity: patterns, causes and consequences. Trends in Ecology & Evolution 8:298-301.
- Lamoreux, J., H. R. Akçakaya, L. Bennun, N. J. Collar, L. Boitani, D. Brackett, A. Bräutigam, T. M. Brooks, G. A. B. Fonseca, and R. A. Mittermeier. 2003. Value of the IUCN Red List. Trends in Ecology & Evolution 18:214–215.
- Lande, R. C. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist 142:911–927.
- Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. Researches on Population Ecology 40:259-269.
- Legendre, S., J. Clobert, A. P. Møller, and G. Sorci. 1999. Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerines introduced to New Zealand. The American Naturalist 153:449–463.
- Lomolino, M. V., and R. Channell. 1995. Splendid isolation—patterns of geographic range collapse in endangered mammals. Journal of Mammalogy 76:335-347.
- Ludwig, D. 1996. Uncertainty and the assessment of extinction probabilities. Ecological Applications 6:1067–1076.
- Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? Ecology 80:298-310.
- Lynch, M., and J. L. Blanchard. 1998. Deleterious mutation accumulation in organelle genomes. Genetica 103:29–39.

Lynch, M., and R. Lande. 1998. The critical effective size for a genetically secure population. Animal Conservation 1:70–72.

- Mace, G. M. 2000. Summary of the results of the review of IUCN Red List categories and criteria 1996-2000. Pages 57-61 in C. Hilton-Taylor, editor. 2000 IUCN Red List of threatened species. International Union for the Conservation of Nature, Gland, Switzerland, and Cambridge, United Kingdom.
- Mace, G. M., and J. E. M. Baillie. 2007. The 2010 biodiversity indicators: challenges for science and policy. Conservation Biology 21:1406– 1413.
- Mace, G. M., and E. J. Hudson. 1999. Attitudes toward sustainability and extinction. Conservation Biology 13:242–246.
- Mace, G. M., and R. Lande. 1991. Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. Conservation Biology 5:148-157.
- Mace, G. M., and S. N. Stuart. 1994. Draft IUCN Red List categories. Species 21/22:13-24.
- Mace, G. M., N. Collar, J. Cooke, K. Gaston, J. Ginsberg, N. Leader-Williams, M. Maunder, and E. J. Milner-Gulland. 1992. The development of new criteria for listing species on the IUCN Red List. Species 19:16–22.
- Mace, G. M., H. P. Possingham, and N. Leader-Williams. 2007. Prioritizing choices in conservation. Pages 17–34 in D. W. Macdonald, and K. Service, editors. Key topics in conservation biology. Blackwell Publishing, Oxford, United Kingdom.
- Mangel, M., and C. Tier. 1994. Four facts every conservation biologist should know about persistence. Ecology 75:607-614.
- Matsuda, H., T. Yahara, and Y. Uozumi. 1997. Is tuna critically endangered? Extinction risk of a large and overexploited population. Ecological Research 12:345–356.
- Matsuda, H., Y. Takenaka, T. Yahara, and Y. Uozumi. 1998. Extinction risk assessment of declining wild populations: the case of the southern bluefin tuna. Researches on Population Ecology 40:271-278.
- Maurer, B. A. 1994. Geographical population analysis: tools for the analysis of biodiversity. Blackwell Scientific, Oxford.
- McCallum, H. 2007. Distribution and impacts of Tasmanian devil facial tumor disease. Ecohealth 4:318–325.
- McGowan, P., and M. Gillman. 1997. Assessment of the conservation status of partridges and pheasants in South East Asia. Biodiversity and Conservation 6:1321-1337.
- Millennium Ecosystem Assessment. 2005. Ecosystems and human wellbeing: biodiversity synthesis. World Resources Institute, Washington, D.C.
- Miller, R. M., et al. 2006. Extinction risk and conservation priorities. Science 313:441.
- Miller, R. M., et al. 2007. National threatened species listing based on IUCN criteria and regional guidelines: current status and future perspectives. Conservation Biology 21:684-696.
- Munton, P. 1987. Concepts of threat to the survival of species used in Red Data Books and similar compilations. Pages 71–111 in R. Fitter and M. Fitter, editors. The road to extinction. International Union for the Conservation of Nature, Gland, Switzerland.
- Musick, J. A. 1999. Criteria to define extinction risk in marine fishes. Fisheries 24:6-14.
- Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenberg. 1995. Population dynamics of exploited fish stocks at low population levels. Science 269:1106–1108.
- O'Grady, J. J., M. A. Burgman, D. A. Keith, L. L. Master, S. J. Andelman, B. W. Brook, G. A. Hammerson, T. Regan, and R. Frankham. 2004. Correlations among extinction risks assessed by different systems of threatened species categorization. Conservation Biology 18:1624– 1635.
- Osborne, R. 1995. The world cycad census and a proposed revision of the threatened species status for cycad taxa. Biological Conservation 71:1-12.
- Owens, I. P. F., and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced

predators. Proceedings of the National Academy of Sciences of the United States of America 97:12144-12148.

- Possingham, H. P., S. J. Andelman, M. A. Burgman, R. A. Medellin, L. L. Master, and D. A. Keith. 2002. Limits to the use of threatened species lists. Trends in Ecology & Evolution 17:503–507.
- Prakash, V., D. J. Pain, A. A. Cunningham, P. F. Donald, N. Prakash, A. Verma, R. Gargi, S. Sivakumar, and A. R. Rahmani. 2003. Catastrophic collapse of Indian white-backed *Gyps bengalensis* and long-billed *Gyps indicus* vulture populations. Biological Conservation 109:381–390.
- Purvis, A., G. M. Mace, and K. E. Jones. 2000. Extinction. BioEssays 22:1123-1133.
- Regan, T. J., M. A. Burgman, M. A. McCarthy, L. L. Master, D. A. Keith, G. M. Mace, and S. J. Andelman. 2005. The consistency of extinction risk classification protocols. Conservation Biology 19:1969–1977.
- Reynolds, J. D., N. K. Dulvy, N. B. Goodwin, and J. A. Hutchings. 2005. Biology of extinction risk in marine fishes. Proceedings of the Royal Society B 272:2337-2344.
- Richter-Dyn, N., and N. S. Goel. 1972. On the extinction of a colonising species. Theoretical Population Biology 3:406-433.
- Rodrigues, A. S. L., J. D. Pilgrim, J. F. Lamoreux, M. Hoffmann, and T. M. Brooks. 2006. The value of the IUCN Red List for conservation. Trends in Ecology & Evolution 21:71–76.
- Rodríguez, J. P. 2002. Range contraction in declining North American bird populations. Ecological Applications 12:238–248.
- Rodríguez, J. P., F. Rojas-Suarez, and C. J. Sharpe. 2004. Setting priorities for the conservation of Venezuela's threatened birds. Oryx 38:373– 382.
- Sala, O. E., et al. 2000. Biodiversity—global biodiversity scenarios for the year 2100. Science 287:1770-1774.
- Samways, M. J. 2006. National red list of South African Odonata. Odonatologica 35:341-368.
- Seal, U. S., T. J. Foose, and S. Ellis-Joseph. 1994. Conservation assessment and management plans (CAMPs) and global captive action plans (GCAPs). Pages 312–325 in P. J. Olney, G. M. Mace, and A. T. C. Feistner, editors. Creative conservation—the interactive management of wild and captive animals. Chapman & Hall, London.
- Seddon, M. B. 1998. Red listing for molluscs: a tool for conservation? Journal of Conchology (Special Publication) 2:27-44.
- Simberloff, D. 1986. The proximate causes of extinction. Pages 259–276 in D. M. Raup and D. Jablonski, editors. Patterns and processes in the history of life. Springer-Verlag, Berlin.
- Sorci, G., A. P. Møller, and J. Clobert. 1998. Plumage dichromatism of birds predicts introduction success in New Zealand. Journal of Animal Ecology 67:263–269.
- Soulé, M. E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pages 151-169 in M. E. Soulé and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachusetts.
- Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783-1786.
- Taylor, B. L. 1995. The reliability of using population viability analysis for risk classification of species. Conservation Biology 9:551-558.
- Taylor, B. L., and T. Gerrodette. 1993. The uses of statistical power in conservation biology: the vaquita and the spotted owl. Conservation Biology 7:489–500.
- Thuiller, W. 2007. Biodiversity—climate change and the ecologist. Nature 448:550-552.
- Todd, C. R., and M. A. Burgman. 1998. Assessment of threat and conservation priorities under realistic levels of uncertainty and reliability. Conservation Biology 12:966-974.
- Webb, G. J. W., and E. Carrillo. 2000. Risk of extinction and categories of endangerment: perspectives from long-lived reptiles. Population Ecology 42:11-17.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126-2128.