

CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES
OF WILD FAUNA AND FLORA



Joint meeting of the Animals and Plants Committees
Shepherdstown (United States of America), 7–9 December 2000

Background to IUCN's system for classifying threatened species*

I. Introduction

In 1994 a new set of rules were adopted by IUCN - The World Conservation Union for listing species in Red Lists of threatened species and in Red Data books. This new, quantitative system replaced a set of qualitative definitions in place since the early 1960's and which had become familiar and been used widely in scientific, political and popular contexts as a means of highlighting the world's most threatened species. The development the IUCN criteria took over five years from first proposals to formal adoption by IUCN. This paper provides the philosophical and technical background to their development and discusses some fundamental aspects of the system.

II. Background to red listing

Red Lists are intended both to raise awareness and to help to direct conservation actions. According to IUCN (1996), the formally stated goals of the Red List are (1) to provide scientifically-based information on the status of species and subspecies at a global level, (2) to draw attention to the magnitude and importance of threatened biodiversity, (3) to influence national and international policy and decision-making, and (4) to provide information to guide actions to conserve biological diversity. To meet the first two of these goals the classification system should be both objective and transparent; it therefore needs to be inclusive (i.e. equally applicable to a wide variety of species and habitats), standardised (to give consistent results independent of the assessor or the taxon being assessed), transparent, accessible (a wide variety of different people can apply the classification system), scientifically defensible and reasonably rigorous (it should be hard to classify species without good evidence that they really are or are not threatened). The application of a consistent system also has the benefit that changes in the list over time can be used as a general indicator of the changing status of biodiversity worldwide.

The third and fourth stated goals of the Red List mean that it needs to influence policy and decision-makers: the challenge here is more complicated. Effective conservation actions generally take place nationally and locally and not at the global level. There are very few mechanisms to conserve species above the national level. Even the Convention on Trade in Endangered Species (CITES) and the Convention on Biological Diversity (CBD), which are global agreements among countries, rely on implementation within countries for

* This document has been prepared by IUCN.

their effectiveness. The Red List is therefore intended to focus national and local conservation actions on the species that most need support. However, it is important to recognise that for various reasons the highest conservation priorities within countries or regions may not simply be the most threatened species found in that region (Gardenfors, 1996). Certain species may be *relatively* secure within a politically defined area but nevertheless be at risk globally, whereas other species that are globally relatively secure may be at the edge of their geographic range and hence be highly threatened within a region. For this reason, the role of global red lists within countries must simply be to give shape and force to conservation planning and help set local actions in a global context. There are various ways in which countries might choose to use global information in their own assessments (Avery *et al.*, 1995; Warren *et al.*, 1997) and so far IUCN has provided no more than general guidance (Gardenfors, 1996; IUCN, 1994).

A further consideration is that global lists of threatened species do not provide a simple assessment of global conservation *priorities* amongst those species. Whilst a threat assessment is a necessary part of any conservation priority assessment, it is not on its own sufficient. Priority-setting should involve many other considerations. These might include assessments of the likelihood of successful remedial action for a species, of the wider benefits for biodiversity that will accrue from directed conservation actions (e.g. for other species within the region, the status of the habitat or ecosystem), and of political, economic and logistic realities. Under some circumstances additional factors are also incorporated in priority assessments, such as the evolutionary distinctiveness of the species (Vane-Wright, Humphries & Williams, 1991), the status of existing protection measures, actual or potential economic value, ecological specialisations of particular note, and the level of information on the species (Collar *et al.*, 1992; Mace, 1995; Millsap *et al.*, 1990; Molloy & Davis, 1992).

III. Development of the new criteria 1989-1994

In 1988 the SSC Steering Committee requested the preparation of a discussion paper and invited a group of scientists within and outside SSC to contribute. In response, draft proposals were prepared and circulated within IUCN during 1989. Reviews of and revisions to these papers led to a final specific proposal which was published in 1991 (Mace & Lande, 1991). This included new quantitative definitions for the threat categories of 'Critical', 'Endangered' and 'Vulnerable' as well as a set of criteria for qualification. Mace and Lande (1991) emphasised that their proposal was mainly appropriate for vertebrates, but suggested that a similar approach could be taken to develop simple criteria for other major taxa. They also outlined some fundamental objectives for a new system, and the background rationale for a system of three categories reflecting increasing levels of risk over decreasing time scales. In the Mace and Lande (1991) proposal, the categories were defined precisely in terms of extinction risk, but a set of criteria based around population sizes, population fragmentation and observed or projected declines in abundance were developed that equated approximately to that level of risk.

This proposal was intended for review and development but was immediately applied to a number of animal groups, in particular through a series of Conservation Assessment and Management Plan workshops organised by the Conservation Breeding Specialist Group of SSC (Seal, Foose & Ellis-Joseph, 1994), and there was also a submission to extend the new system for listing species in the Appendices to CITES. The SSC decided that further work was needed to test and validate the proposals and to broaden their applicability. During 1992, comments were sought from a variety of experts and two workshops were held in November 1992 (Mace *et al.*, 1992). Prior to the workshops background papers reviewing conservation priority and threat assessment systems used elsewhere were made available to participants. Inputs on the definition and measurement of extinction and extinction risk were also sought from academic biologists to complement the viewpoints from conservation practitioners. At the first of the workshops biologists and conservation practitioners with expertise on different major taxonomic groups, drew up proposals for criteria for higher vertebrates, lower vertebrates, invertebrates and plants, using the Mace and Lande (1991) approach as a template. At the second workshop more general topics relating the development and use of threatened species lists in conservation management and in legislation were discussed. In particular, there seemed to be a congruent set of requirements for the IUCN Red List and for biological criteria for listing species in the appendices to CITES.

At the end of the workshops, four sets of draft criteria had been prepared, appropriate to the major taxonomic groupings, and a small drafting group of eight was appointed by SSC to continue the process. This group met three times during late 1992 and January 1993. It was apparent that there was a great deal of overlap between the four sets of criteria and quite soon the decision was taken to merge them into a single set that should be applicable to all species. This means that the different criteria operate as a set of independent filters; so long as a species can qualify by meeting the threshold values for at least one criterion it is unimportant that other criteria are not met, or might never even be appropriate. This concept has proved difficult to communicate; the immediate reaction of many users continues to be that the system is flawed because the same set of criteria can never be appropriate for all species (e.g. Kuzmin *et al.*, 1998).

The first new version of the threat criteria from the drafting group was reviewed by workshop participants in February 1993, and after some further revisions the proposal (now called version 2.0) was published in *Species* (the IUCN/SSC members journal) in June 1993 (Mace *et al.*, 1992)¹. *Species* is circulated to all 7000 SSC members, and comments and criticisms were sought. At the same time, a number of taxon specialist groups were asked to undertake a more formal test of the criteria, report the results and comment on ease-of-use and applicability of the system. By the end of August 1993 over 70 items of correspondence had been received, including trial results from application of the draft criteria to over 500 species from a wide variety of taxonomic groups (e.g. bryophytes, orchids, cacti, cycads, conifers, molluscs, damselflies and dragonflies, butterflies, freshwater fish, 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 consequently prepared towards 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 Buenos Aires in January 1994. Feedback from IUCN members and from elsewhere continued into early 1994, and more revisions were made for a final version (version 2.2) that was again published in *Species* (Mace & Stuart, 1994). This version was very close, although not identical, to the version finally accepted by IUCN in November 1994, and was used for the preparation of *Birds to Watch 2* (Collar, Crosby & Stattersfield, 1994).

The version accepted by IUCN Council (version 2.3) was published as a booklet (IUCN, 1994). This includes the formal descriptions of categories, criteria, rules and definitions. Although shorthand versions have been published elsewhere, users have always been advised to consult this document, or the web-based documentation (<http://www.iucn.org/themes/ssc/redlists/ssc-rl-c.htm>) as a source since the information is specific and complete, whereas condensed versions are open to misinterpretation.

IV. Assessing extinction risk - background to the criteria

The IUCN Red List categories are intended to reflect the likelihood of a taxon going extinct under current circumstances. To estimate this likelihood it is necessary to consider both extrinsic threats to species as well as the biological characteristics that increase their vulnerability to extinction. Here we review the approaches to extinction risk assessment that are used in the development of the IUCN system.

The major processes driving extinction are anthropogenic and result from habitat loss, over-exploitation, introduced species and the interactions between these (Diamond, 1989). There are many sub-types within each of these main (see Lande, 1998). These processes may be regarded as the extrinsic drivers, the ultimate causes of extinction as described by Simberloff (1986), or the agents behind the 'declining population paradigm' described by Caughley (1994). It is these processes that make the current extinction spasm so distinct from periods of background extinction in the fossil record, which are several orders of magnitude lower in frequency (May, Lawton & Stork, 1995; Pimm *et al.*, 1995).

Understanding the nature of the current anthropogenic threatening processes is essential to assessing extinction probabilities because of their overriding significance, and because their impacts may be expected to change non-linearly with increasing human population density. Ultimately the effects of these extrinsic drivers on a species is variable and depends on their ecology, life history, physiology or distribution. The

¹ Although this publication is dated 1992, it was in fact printed and distributed in the middle of 1993.

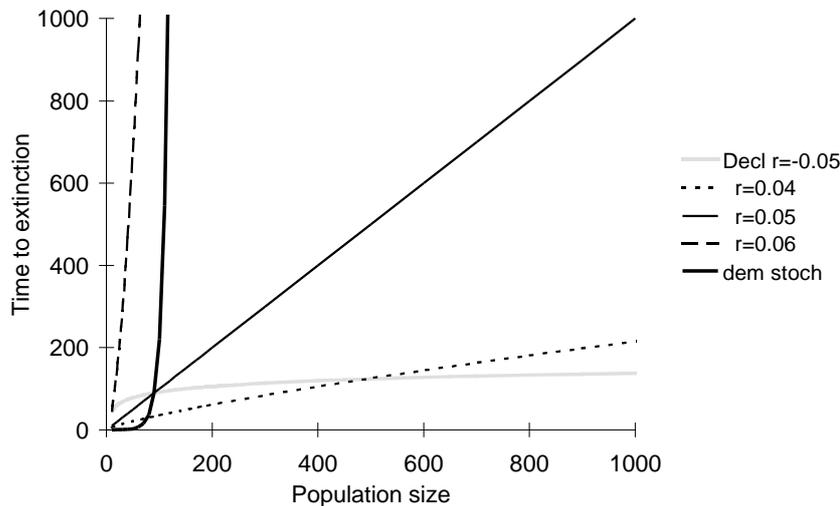
characteristics of extinction-prone species has have been more thoroughly investigated by research biologists than have the effects of the external drivers and the interactions between the two (Caughley, 1994), leading to some debate about the relative importance of each. However, it is clear that both approaches are needed (Hedrick *et al.*, 1996) if we are to improve the reliability of predictions about extinction risk.

Our knowledge of the nature and causation of species' extinctions can be informed by several kinds of evidence. First, many empirical studies have identified characteristics of extinction-prone species. Local extinction has been shown to be higher for species that have restricted ranges or occupy a small number of sites (Gaston, 1994b; Gaston & Blackburn, 1996b; Gaston & Chown, 1999; Hanski, 1982; Happel, Noss & Marsh, 1987; Simberloff & Gotelli, 1984; Thomas & Mallorie, 1985), are local endemics (Cowling & Bond, 1991; Terborgh & Winter, 1980) or have low abundances, high temporal population variability and poor dispersal (Diamond, 1984; Gaston, 1994b; Karr, 1982; Newmark, 1991; Pimm, Jones & Diamond, 1988). These studies are all open to the criticism that they may only be investigating correlates of extinction-prone characteristics, since body size, dispersal ability, range size, population variability and local population density are all interrelated (Gaston, 1994b; Gaston & Blackburn, 1996a; Gaston & Blackburn, 1996b; Gaston & Lawton, 1988; Gaston & McArdle, 1994; Lawton, 1995; McArdle, Gaston & Lawton, 1990; Pimm, 1992). An additional problem is that the measurement of abundance, population variability, range area, and their comparison across spatial scales all present some methodological difficulties (Gaston, 1991; Gaston, Blackburn & Gregory, 1999; Gaston & McArdle, 1994). However, in studies where inter-relationships among life history traits and the geographical sampling can be controlled for, independent associations with population density, range size and habitat and diet specialisation have been shown (Foufopoulos & Ives, 1999; Purvis *et al.*, 2000).

The response of a species to a threat is more complicated: it will depend on both with its life history and the environmental circumstances. For example, the stability of fluctuating populations is reduced by exploitation (Beddington & May, 1977), the response of primates to logging is a function of their home range size and the latitude at which they live (a correlate of habitat variability) (Harcourt, 1997), land bridge island reptiles are more likely to go extinct if they have low abundance and high habitat specialisation (Foufopoulos & Ives, 1999), and extinction of carnivores within reserves is higher for those with large home ranges (Woodroffe & Ginsberg, 1998).

Second, there are some useful insights from theoretical work on times to extinction. It can be shown that small populations are more extinction-prone because of their susceptibility to demographic stochasticity (Goodman, 1987; Richter-Dyn & Goel, 1972), the accumulation of recessive deleterious alleles under inbreeding (Soule, 1980), the loss of quantitative characters that allow adaptation, and the accumulation of mildly deleterious mutations (Frankham, 1995a; Hedrick & Miller, 1992). Lande (1998) has reviewed all of these predictions in terms of the minimum viable population size that they imply.

Figure 1. Relationships between extinction time and population size differ depending on the process that is involved in the decline. This figure compares the shape of the relationships under demographic stochasticity (dem stoch), deterministic decline at $r = -0.05$; and environmental variation where environmental variance = 0.05 and $r = 0.04$, $r = 0.05$ and $r = 0.06$. The effects of demographic stochasticity are serious at very small population sizes but then become insignificant. The impact of environmental stochasticity increases as the ratio of environmental variance to population growth rate r increases. Deterministic exponential declines are always serious whatever the population size.



Demographic stochasticity is unlikely to be important for any population that has more than 100 individuals, but random environmental variation or catastrophes are important for populations of all sizes, and become more significant as the extent of variation becomes large in relation to the population growth rate (Lande, 1993a) (see Figure 1). Accumulation of deleterious recessive alleles is a short-term genetic problem which means that to safeguard genetic variability in species over hundreds of years will require minimum effective population sizes of at least 50. Since effective population size is usually only about 10 to 20% of the actual number of individuals (Frankham, 1995b; Mace & Lande, 1991) this number should be a minimum of 250 to 500 individuals. Larger populations are needed to preserve quantitative trait variation - to maintain high levels (>90%) over thousands of years will require minimum effective population sizes of at least 5000, and to prevent the accumulation of mildly deleterious mutations over tens of thousands of years will require minimum effective population sizes of around 10,000 to 100,000. Because of difficulties in estimating key parameter values for these calculation (Franklin & Frankham, 1998; Lynch & Lande, 1998) the critical population sizes from these theoretical studies are best interpreted as guides to the relative importance of different characteristics rather than real thresholds for management (Lande, 1998).

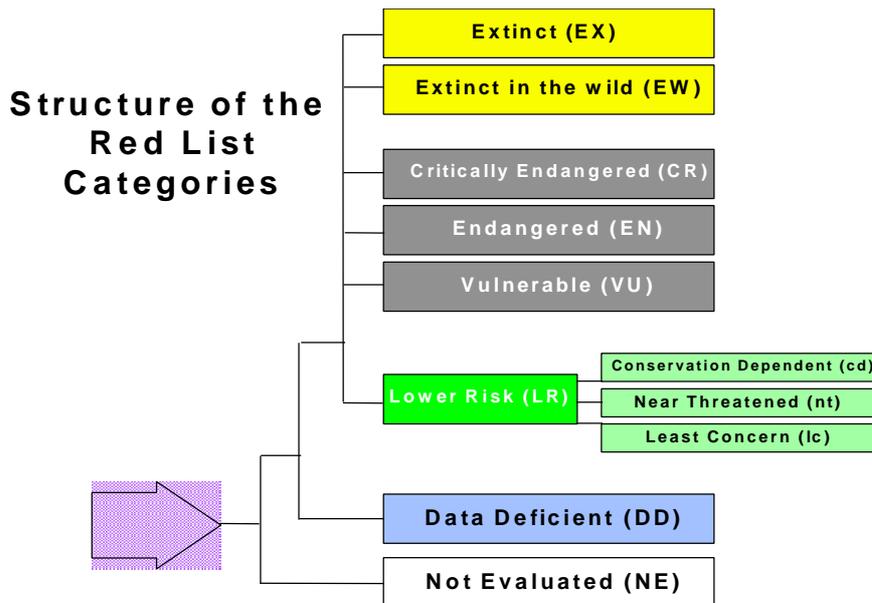
These observational, correlational, empirical and theoretical studies provide the starting points for developing more objective criteria for estimating extinction risk. However, it is clear that extinction processes comprise a complicated set of interacting factors that would be impossible to simplify appropriately. Furthermore, since the driving processes often dominate extinction risks (Harcourt, 1995; Simberloff, 1986) it is more relevant to reflect symptoms rather than theoretical derived thresholds. Consequently, the new threat criteria are based on the detection of symptoms, not causes or consequences, and 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 cases 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).

V. The IUCN categories and criteria

1. The Categories of Threat

The complete set of rules for the IUCN system is reproduced in the Appendix. There are eight categories of threat (Figure 2).

Figure 2. Schematic representation of the IUCN classification scheme.



Under the system, all species can be classified into one, and only one, category. There are essentially three different classification systems in the new criteria. The first is the distinction between Not Evaluated and all the other categories (the first dichotomy in Figure 2). Not Evaluated is a category for all species for which no classification under the system has been attempted. This category is useful because without it there is potential confusion about the status of species that are not included in Red Lists; they might be either be not threatened or not evaluated. The Not Evaluated category is also used to track the movement of species into more meaningful classifications as information accumulates.

The second dichotomy in Figure 1 is the distinction between species for which a threat category has been allocated, and those for which information is inadequate to make a classification (Data Deficient). The category Data Deficient is not a category of threat, but simply states that there is insufficient information to make an assessment against the criteria.

The third classification is the main purpose of the system - the determination of threat level. There are two categories for extinct species - Extinct, and Extinct in the Wild, but the definition of extinction is the same for both. Unlike previous definitions of Extinct which relected the time since individuals of the species were last seen, the new definition places emphasis on whether surveys have taken place at appropriate times and places. Therefore, it is possible for taxa to be categorised as Extinct (or Extinct in the Wild) very soon after living individuals have been observed, but only if there is good evidence that they cannot still persist. However, the intention is generally to be extremely precautionary about categorising taxa as Extinct. An erroneous extinction classification can have several deleterious consequences. It can bring the list into disrepute, but also, and perhaps more seriously, once a species is believed to be extinct, there can be little

justification for conservation funding or for habitat protection and, moreover, there is little effort put into searching any more (Collar, 1998). Recently MacPhee (1999) has suggested new criteria for categorising species as extinct. Their proposals slightly misrepresent the current IUCN definition of extinction, and are thus perhaps less divergent than they suggest. In addition, they place more importance on taxonomic validity than would be appropriate for conservation planning where urgent actions might need to be taken in the absence of formal descriptions and documentation of specimens.

Within the threat-level classification there are three categories for threatened species (Critically Endangered, Endangered and Vulnerable). The categories are defined qualitatively by decreasing probabilities of extinction over increasing time scales, but are explicitly defined by five criteria (A to E). The threat categories are nested so that any taxon 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 taxon needs to meet any one of five criteria. Not meeting other criteria has no bearing on the matter. One of these criteria, criterion E, is an extinction risk probability which results from undertaking some kind of quantitative analysis. This criterion is equivalent to the definition of extinction risk that was used in the Mace and Lande (1991) criteria. The decision to move this from its status as a definition for a category of threat to one of five criteria was made because of the difficulties that would be involved in showing that the criteria equated to the extinction risk probabilities given in any of the categories of threat. It was also recognised that the quantitative assessment of extinction risk could be non-precautionary, especially using standard PVA models (Ludwig, 1999; Taylor, 1995). This is particularly a problem where assessors use inappropriate PVA analyses which do not incorporate all relevant risk factors to make an assessment (Akçakaya & Burgman, 1995; Beissinger & Westphal, 1998; Harcourt, 1995). The criteria for assignment to a threat category are discussed in more detail below.

The category of Lower Risk is used for species that do not meet any of the criteria for Vulnerable. However, many species that qualify for Lower Risk may not have been assessed against some of the criteria, because of a lack of relevant information. Since these species cannot be assessed against other criteria the decision as to whether these are categorised as Lower Risk or Data Deficient may be a difficult one. In essence it will depend on the judgement that an assessor makes about the relevance of the assessed versus un-assessed criteria. In contrast, an assessor cannot ignore the listing of a species in a category of threat, even if they believe that the criterion that triggered that listing is not relevant for the taxon that they are considering.

2. Criteria for Critically Endangered, Endangered and Vulnerable

a. Criterion A - high decline rate

Criterion A is designed to identify species in actual or potential rapid decline, ie species that are facing threatening processes that involve high rates of loss of individuals from the population. Unlike the other criteria there is no numerical limit on the population size or the geographic range area of the species - the criterion is intended to detect 'declining population' rather than 'small population' extinction phenomena (*sensu* Caughley 1994). The role of criterion A is important in the IUCN system, since widespread or abundant populations could not otherwise be listed as threatened until they reached the critical cut-off values for area or population in criteria B and C.

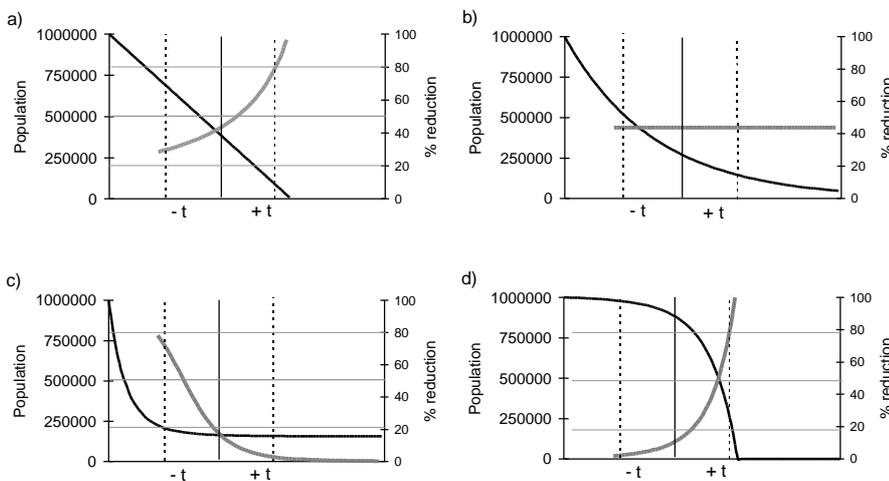
The principle of Criterion A is illustrated in Figure 3. An estimate of current population size is compared with an estimate from the past or into the future, and the change over the specified time period t is compared with threshold values for Critically Endangered, Endangered and Vulnerable. Population size is adjusted using the measure 'Mature individuals', which is specifically defined in the criteria to reflect the size of the actual or potential breeding population. Since individuals of different species have very different average life spans (from hours in mayflies to millennia in some trees), the period over which declines are measured is expressed in generation lengths. Generation length acts as a surrogate for turnover rates within populations. Long-lived species will be at greater risk from low annual adult mortality rates (measured as percentage loss per year) than will short-lived species because breeding adults experience this mortality over more years. Conversely, a long lived species declining at the same rate (measured as percentage change per generation) as a short-lived one will show smaller reductions over time (measured in years). However, the time window over which

declines are measured is set to a minimum of 10 years because measuring changes over shorter time periods would be practically difficult and would also not reflect human timescales and human effects.

The decline, measured as percentage loss, can be estimated in the past (Criterion A1), or the future (Criterion A2). A species may qualify by A1, A2 or both. Because of the difficulties of estimating population sizes in most natural populations, the criteria allow the assessor to use various kinds of information to estimate the decline in population size, but require such information to be made explicit so that users can see the basis for the classification. This is achieved by listing as many of the subcriteria (a) to (e) as are appropriate. Criterion A1 listings may be based on direct observation (population counts of some kind), which is obviously not feasible for Criterion A2 listings. For either A1 or A2 listings declines may be based on indices of abundance (b). This may be appropriate where assessors cannot estimate population size but have other information that is closely related to it. Sightings, catch per unit effort, and other such indices may be used (Seber, 1982; Sutherland, 1996). Assessment of threatening processes may also be used for Criterion A listings, based on loss of habitat (c), levels of direct or indirect exploitation (d), and the effects of introduced taxa, hybridisation, pathogens, pollutants, competitors or parasites (e). However, assessors need to use such indirect evidence cautiously. For example, a measured decline in habitat area cannot be straightforwardly translated to an equivalent decline in population size, especially if it is edges or lower quality habitat areas that are lost.

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 % of the starting number (grey solid line). -t and +t represent the past and future points where assessment is made compared to the present, represented by a solid vertical line.

(a) a constant number of individuals are lost in each time period; (b) a constant proportion of individuals are lost in each time period; (c) a declining proportion are lost in each time period; (d) an increasing proportion are lost in each time period.



The criteria are unspecific about how information on temporal changes in population size should be used to calculate a past decline rate or project a future decline. Several points are important here. First, depending on the situation it may be appropriate to use some statistical method to calculate the decline rate. For example, where there is a series of population estimates over time the assessor might fit a least-squares regression line and estimate the decline rate from the slope of the line. However, it may often be both inappropriate and impractical to do this. Where populations show non-linear trends within the three generation assessment period, such as an increase followed by a decrease, fitting such a regression line could be misleading (Usher, 1991). Second, for very many species there is no systematic information on population size and the assessor

may need to make a determination of trends based on extremely limited information. Often, the best that can be done here is to use the estimated number at the beginning and end of the three generation census period. The potential problems of this approach are self-evident, but it is perhaps less obvious that even with apparently good information it may be very difficult to make a robust estimate of population trends. Accurate measurements of changes in population size depend critically on the quantity and quality of the data available (Taylor, 1995). Over limited time-spans or with small numbers of surveys it is possible to either 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) this does not solve the problem in cases where the situation is both extremely uncertain and serious (Colyvan *et al.*, 1999). In the presence of uncertainty it may be necessary for the assessor, who should have to hand the best information available, to use both formal data analysis and expert judgement (Colyvan *et al.*, 1999). Methods and techniques for doing this are now being made available (Akcakaya *et al.*, in press).

The assessor will often have no direct information on changes in population size and be compelled to make an assessment of past or future declines based on information about the threatening processes. Careful analysis is needed to estimate population declines from such processes, since the relationship is generally not simple, and populations may compensate or collapse according to the nature of the process. Figure 3 illustrates a variety of simple decline trajectories where population decline rates are either increasing (a and d), constant (b) or decreasing (c). Each of the graphs illustrates both a change in population size (solid black line) and the decline rate that would be estimated at each point in time (solid grey lines). If the vertical line represents the present then the criteria require a measure of the decline that has occurred in the past 10 years or 3 generations (whichever is longer), represented as the line at $-t$, or the decline that is expected in the next 10 years or 3 generations (whichever is longer), represented by the line at $+t$. There are various ways in which systematic declines might proceed over these periods.

Figure 3(a) shows a population that is declining by a constant amount each year so that as it becomes smaller the decline rate increases. This might be the situation where over-exploitation, interspecific competition or predation led to population reduction, but the amount of extra mortality was constant, perhaps related to the size of the predator or competitor population. Here, past decline rates allow the species to qualify at Vulnerable (decline $>20\%$), but future declines projected to continue on the same basis give an Endangered ($>50\%$) categorisation. If declines continued, this population would soon qualify for Critically Endangered ($>80\%$ decline), before going Extinct. In Figure 3(b) the extra mortality caused by the threat is a constant proportion of the population size (i.e. as the population size decreases the amount of extra mortality decreases proportionately and the decline rate is constant). This might be the case where the effects of exploitation, predation or competition are directly related to the abundance of the species. The population in Figure 3(b) always qualifies for Vulnerable, and will never qualify for any higher threat category under criterion A, until it goes Extinct. In practice, a species showing this pattern would qualify for higher threat categories under criteria B, C or D once the population size or the geographic range reached low enough levels to meet the thresholds in those categories. The example in Figure 3 © shows another case where the extra mortality declines over time, but here the decline rate is decreasing. This means that ultimately the extra mortality ceases altogether and the population can stabilise and may even recover. The decline rate progressively decreases so that the species that originally qualified as Critically Endangered moves through Endangered and Vulnerable until eventually it is non-threatened. This pattern is expected under a variety of situations - most commonly this is the intention of managed harvesting programmes which reduce the population size until the density at which productivity is maximised is reached, the harvest is then stabilised at a sustainable level and there should be no further decline in population (Milner-Gulland & Mace, 1998).

Finally, Figure 3(d) shows the population depletion and decline rate for a population where the rate of decline is increasing exponentially 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. In addition, increased decline with smaller populations might also be expected where inverse density dependence (known as Allee effects or depensation) is operating (Courchamp, CluttonBrock & Grenfell, 1999; Myers *et al.*, 1995). In this situation the decline rate increases exponentially, so that in a very short space of time the species moves from non-threatened through Vulnerable, Endangered and Critically Endangered until it goes Extinct. In practice this pattern has been seen in populations of African elephants (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*) (Leader-Williams, Albon &

Berry, 1990; Milner-Gulland & Beddington, 1993), although in these cases the rate of decline slows at very low population sizes so that the species may stabilise at a new but very low level, rather than go extinct.

The four simple kinds of decline dynamics discussed here are obviously a small subset of the possible patterns that might be seen in real cases, but they illustrate some more general points about Criterion A. The array of plausible patterns of decline and the requirement to provide to apply the criteria precautionarily mean that the choice of threshold values is a difficult balance between quantities that will detect species in decline well before they reach critically low levels and that will often falsely list species that are nearing the end of a decline that is slowing and will soon cease. The decline rates that were selected in the IUCN criteria do not therefore equate to a simple steady loss from some large population size (Gillman & Silvertown, 1997; Matsuda, Yahara & Uozumi, 1997). Instead, the approach was taken that many declines seen in species of conservation concern may approximate to the patterns in Figure 3(a) and 3(d). The problem is that threshold values for decline rates then have to be set quite low and this can lead to misleading listings of species that are following the patterns seen in Figure 3(b) and 3(c). However, if the decline rate is slowing and the population is stabilising or even recovering, then it will soon cease to qualify under Criterion A thresholds. The decision was made to let the listing be determined solely by the data on decline rates, though recognising that sometimes there might be transient false listings until the population stabilised or the decline rate dropped sufficiently that the criterion was no longer met. This has led to some controversy especially about the status of wild species that are the focus of managed harvests (Mace & Hudson, 1999; Matsuda et al., 1998; Matsuda et al., 1997) and it has been suggested that resilience should be more explicitly factored into the criteria (Musick, in press). Conversely, other commentators have criticised the criterion because 'depleted' species eventually fall out of the threatened list, even though their numbers are dramatically reduced.

b. *Criterion B - small range area and decline*

Criterion B allows a species to qualify as threatened when its geographical distribution is very restricted and when other factors suggest that the species is at risk. The origins of this criterion trace back to the plant working group in one of the original workshops that IUCN held in 1992. The basis is that for many species there are situations in which population size may not be measurable but where an elevated extinction risk is apparent, as for example when species are restricted to small areas or to habitat remnants that are themselves disappearing. Species restricted to small areas of distribution suffer elevated extinction risks both because these areas can be rapidly and extensively degraded by human activities and through the association with small population sizes. Even though individuals may still be numerous, further loss of habitat can rapidly lead to extinction. The drafting group considered that this criterion was relevant not only to plants; many other species that live at high densities within restricted areas may be similarly affected.

This criterion does not simply use range area as a surrogate for population size. Although there is a very broad positive correlation across species between total geographic range size and population numbers, there is much variation and the pattern of this relationship alters according to the spatial scale at which it is assessed (Gaston, 1994b). In some cases, species may qualify for both population size and range size criteria, but more often we expect the two measures to operate independently. Many species that qualify as threatened under criterion B will be species that could never qualify on the basis of population size. Conversely, some species - marine mammals, for example, will never qualify under criterion B, however close to extinction they get, because the ranging patterns of individuals will exceed the critical thresholds.

The measurement of range area is complicated (Gaston, 1991; Gaston, 1994a; Gaston, 1994b; Maurer, 1994). The criteria employ two quantities, extent of occurrence and area of occupancy (*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 can be strongly influenced by cases of vagrancy and by marked discontinuities or disjunctions within the overall distribution of a species. These should be excluded. What constitutes a discontinuity or disjunction has deliberately been left vague, but of particular concern here are ranges composed of broad environments that are totally unsuitable for occupancy or often even for dispersal. It would, for example, be inappropriate to include intervening areas of ocean in the estimation of extent of occurrence of a forest-dwelling species occurring at sites on two continents.

The second measure of range area used in the criteria, area of occupancy, quantifies the area within its extent of occurrence over which the species is actually found. No species will occur throughout its extent of occurrence, as none is continuously distributed in space. As applied in the criteria, area of occupancy 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 area of occupancy of a species will be a function of the spatial scale at which it is measured: the finer the resolution the smaller the resultant area (Gaston 1991). Whilst no scale of measurement is specified in the criteria, it is stated that the scale should be appropriate to relevant biological aspects of the taxon, and should be measured on grid squares (or equivalents). The intention here is that scales are used which reflect the movement and/or dispersal patterns of the species of concern, and that exceedingly fine resolutions of measurement are avoided. This solution to the matter of spatial scale is less than ideal, but no simple means of handling this issue more directly was or is now available.

The measurement of both extent of occurrence and area of occupancy has been thought to be 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 river or the intertidal zone) 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 pollution event may easily affect an entire watershed) and so it was felt that no special treatment for species with linear ranges was necessary.

Unlike population decline rates and population sizes, there is no strong theoretical framework whereby given range areas (which for a given size may continue hugely different numbers of individuals) can be associated with different levels of risk of extinction. Therefore, although such a 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 both methodological and biological standpoints. The final decisions were largely made 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 extent of occurrence and area of occupancy (a difference of a factor of 10) in each of the categories Critically Endangered, Endangered and Vulnerable, and cut-offs for the former of 100km², 5000km² and 20,000km². All of these areas, both for extent of occurrence and area of occupancy, are comparatively small, reflecting the fact that only then is range area of itself likely to be associated with high levels of risk of extinction.

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 quite successfully for long periods with small global ranges, and have a small risk of extinction. To qualify under criterion B therefore, a species must also exhibit at least two of three other symptoms of risk. The conditions here are made quite difficult to meet to avoid over-listing: there must be some evidence that the population is (a) in continuing decline, (b) extremely fragmented or limited to a few independent subpopulations, or © subject to extreme fluctuations. All of these conditions will increase the likelihood of extinction based on empirical and theoretical studies (see Pimm, 1992).

There has been commentary on criterion B suggesting that it may be overly inclusive, with the threshold values set too high, so that a large number of species are inappropriately listed as threatened (Keith, 1998). In some cases this criticism results from applying the global criteria at a regional scale. Within a particular geographic or politically defined area it may be the case that all local endemic forms qualify for threatened status using the criteria if the total area under analysis is small, there is little habitat heterogeneity and threats are general across habitats. Obviously such lists that cannot distinguish conservation status among species are not be useful for local conservation planning. However, this does not mean that the criteria are wrongly formulated for a global scale analysis. In contrast we consider that it is reasonable to list all species in restricted habitat areas if that habitat is clearly under threat. 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). However, we see no reason *a priori* why either of these should follow, since the criteria are intended to operate independently of one another and threats are expected to vary between species and habitats.

c. *Criterion C - small population size and decline*

Criterion C traces back to the original proposal by Mace and Lande (1991) and focuses on populations that are numerically small and in continuous decline. This criterion is the most straightforward of all to place in a theoretical framework. The choice of threshold sizes for the number of mature individuals is based around theoretical values for minimum viable populations (see above) which are adjusted to reflect timescales appropriate for the criteria. 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 we know from theoretical studies about the general relationships between population size and time to extinction under various kinds of environmental and demographic stochasticity (Lande, 1993a; Lande, 1998).

A population in continuing decline may immediately qualify if the decline rate meets the threshold values in criterion C1. If a decline is known or expected and is not measurable or not severe enough to meet the threshold in C1, the species may qualify under C2 if its population is known either to be severely fragmented or to exist as a single unit. Species cannot qualify for criterion C simply by meeting the population size threshold and being in decline because this could admit many species that are still numerous and declining very slowly. Indeed, 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 subconditions should not be the same in each (contra Keith, 1998).

d. *Criterion D - Very small population size*

Criterion D is the only criterion that allows species to be listed as threatened without any 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 can alone lead to population extinction (Goodman, 1987; Lande, 1993b); the importance of this circumstance is supported empirically by a number of studies on very restricted populations (Gaona, Ferreras & Delibes, 1998; Kokko & Ebenhard, 1996; Legendre *et al.*, 1999). However, although demographic stochasticity is generally unimportant for populations numbering less than about 100 individuals its deleterious effects are amplified by life history and behavioural differences among species (Legendre *et al.*, 1999; Sorci, Moller & Clobert, 1998). Hence the threshold numbers used in the criteria are larger. For Vulnerable this means that any species with fewer than 1,000 mature individuals can qualify, and 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 (Figure 2).

Criterion D has a sub-criterion D2 that is only present in the category of Vulnerable. D2 allows species to qualify solely on the basis of a very restricted distribution (i.e. it is the range area equivalent of D1). D2 is conceptually distinct, however, since it is implicit in the 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 wording states; "Population is characterised by an acute restriction in its area of occupancy (typically less than 100 km²) or in the number of locations (typically less than 5). Such a taxon would thus be prone to the effects of human activities (or stochastic events whose impacts is increased by human activities) within a very short period of time in an unforeseeable future, and is thus capable of becoming Critically Endangered or even Extinct in a very short period". This sub-criterion has sometimes been misused, mainly because there has been a tendency to apply the guideline numerical thresholds from the first sentence of the definition without reference to the second half. Summary tables of the criteria, such as that published in IUCN (1990), tend only to include the numerical guidelines and this may have increased the extent of misinterpretation.

D2 is not extended into the higher risk categories since it was felt that the justifications for listing on this basis were always going to be rather problematic, and while it could be justified under the precautionary principle at the relatively low levels of risk embraced by Vulnerable, it was unjustifiable for Endangered and

Critically Endangered. Some users believe that D2 should be extended to allow listings higher than Vulnerable for extremely restricted species (Seddon, 1998) while others find D2 overly inclusive and are critical that D2 apparently fails to recognise that for many species rarity is a natural state and only certain kinds of rare species are actually liable to go extinct (e.g. de Lange & Norton, 1998).

e. *Criterion E - unfavourable quantitative analysis*

Criterion E allows the assessor to use any kind of quantitative analysis for assessing the risk of extinction, which is then compared to the extinction risk thresholds given for each of the categories. These thresholds are expressed as the probability of extinction within a time-frame. The time frame is measured in years or generations as in the formulation of criterion A, using whichever of the two is the longer. Justifications for the thresholds are essentially the same as in Mace and Lande (1991), except that the time-frame for Critically Endangered changes from 5 to 10 years; 5 years was felt to be too short to equate with the other criteria.

The term quantitative analysis was chosen carefully to avoid the impression that this criterion necessarily involves a population viability analysis (PVA). In fact, 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 but based on information about the status of the habitat. For example, a species might be endemic to an area and unable to migrate elsewhere for survival, while forestry rights have been sold to allow the entire area to be cleared within 20 years. The species certainly qualifies as Endangered. It may qualify as Critically Endangered if it occupies less than the whole area and there is at least a 50% chance that the critical habitat areas will be cleared in the first 10 years. Many similar cases where criterion E can be used involve land-use changes and expected levels of exploitation. Another useful circumstance could be where there is known to be a high risk of invasion by a species whose presence would be disastrous for the resident species.

More commonly a PVA would be involved in the assessment. No standards are given for the kind of PVA, but the rules dictate that the structure of the model and the data used in the analysis be made explicit. In fact, PVAs have very rarely been used in IUCN assessments (see below) and we believe that this is appropriate in the circumstances. There are several potential problems with the more widespread use of PVA modelling in such assessments. First, despite the requirements that the exercise be made explicit, it is in practice quite difficult to list and justify the background to a PVA analysis without lengthy documentation. Listings under criterion E might then be much less transparent than listings under the 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, though improbable, values in a PVA model. It will be very hard for IUCN to monitor and guarantee standards when accuracy depends on validating many such problematic variables (Ludwig, 1996; Ludwig, 1999; Mangel & Tier, 1994). Finally PVA models may be non-precautionary because in the absence of good information they tend to assume favourable values for key parameters (e.g. Armbruster, Fernando & Lande (1999)). As a result many practitioners have suggested that PVA is best used as a way for 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; Lindenmayer *et al.*, 1993). We concur with this view and recommend use of criterion E for simple and explicit modelling exercises rather than the incorporation of the outcome of detailed multi-parameter species- and habitat-specific models.

VI. Major features of the drafting process

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

1. Accuracy and precision

Alongside the need for an easily applied and objective system was the requirement that the listings be reasonably robust and accurate. Increasingly the conservation status of species is a factor in disputes that are significant both politically and economically, and it is likely that the system on which listings are based will come under close scrutiny, and perhaps legal challenge. Moving from qualitative to quantitative criteria has the counter-intuitive outcome that listings are both more likely to be challenged and harder to support. There is a dilemma here since the new system is a probabilistic assessment (i.e. listing in a threat category means only that there is a specified probability that the species will go extinct within some time-frame).

The categories and criteria were intended to be precautionary and to lead to listings in all cases where the species exhibited symptoms consistent with impending extinction. The categories of threat (Critically Endangered, Endangered and Vulnerable) do not imply an exact extinction risk probability for each species listed within each category. The categories are, as their name suggests, discrete groups. The system is intended to be accurate in that a larger proportion of species listed in higher threat categories are expected to go extinct in shorter periods. We anticipate that these proportions and periods correspond generally with the values given for each category in criterion E, but this cannot be shown to be so. In any case, this is very different from expecting that the extinction risk expressed in criterion E applies to a species that qualifies by any of the other criteria at that level. Therefore the determination that particular listings under criterion A and criterion E are very different is not a relevant criticism (Matsuda *et al.*, 1998; Matsuda *et al.*, 1997). The IUCN categories do not represent any kind of robust prediction about the fate of a particular species but are intended to provide accurate categorisations of species with similar extinction risks.

It is inevitable that species will be listed as at risk yet do not actually go extinct. The system is probabilistic, and so there is only a limited probability that species in any one category will go extinct. Moreover, the system is precautionary and in any risk-averse system it is inevitable that there will be some over-listing (Mace & Hudson, 1999). Finally, the very act of listing species on a Red List should lead to increased conservation and protection, thereby becoming a self-denying prophecy. It was hoped to minimise the number of species that might be falsely listed as threatened but this cannot be achieved without excluding some that *should* be listed. Drawing this line is difficult. We have consistently argued that a Red List categorisation is not a conservation action in itself. The listing should simply indicate that attention to the species is necessary; at that point the relevant bodies and agencies, often with more detailed information at hand, must be prepared to assume responsibility for an appropriate response (Mace & Hudson, 1999).

2. Stochastic threats

The most fundamental feature of the new system is its intention to measure extinction risk, and not other factors, such as rarity, ecological role or economic importance, that are commonly incorporated into conservation priority systems (Burgman *et al.*, 1999; Mace, 1995; Munton, 1987). A consequence is that trends in abundance and range size are generally more important for listing species than are assessments of population size or areas of distribution; projection of future population sizes (under criterion A2) on the basis of the dynamics of known threats is therefore permitted. However, this strategy raises new difficulties because there are various kinds of extinction process, ranging from the highly predictable and deterministic (such as wholesale habitat clearance) to the unpredictable and stochastic (such as invasions, diseases, or political and economic changes affecting a species).

This has led to a debate, which has continued from the earliest stages in the design of the criteria, concerning the correct listing of small and stable versus large but declining populations. In earlier versions, a 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 apparently 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 1994, 1997) and possess life-history characters which 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 to both natural and anthropogenic processes that may suddenly and seriously affect their status. Essentially, 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 very unlikely to go extinct within ecological time-frames. However, without such a category or criterion, many species that are perceived to be key to the overall preservation of biodiversity are only listed alongside the most abundant and widespread forms as 'Lower Risk'.

The decision as to how to deal with these species changed several times throughout the drafting process. The final verdict was to allow a rather restrictive criterion for rare species (criterion D2) under Vulnerable (and not at the higher threat levels), and to place it in one of the existing criteria (criterion D). However, the debate continues, and is again highlighted in the ongoing review of the criteria (see below).

3. Common criteria for all species

A yet more difficult issue was how to ensure that all species, despite their wide variation in life history and ecology might be treated equitably using the criteria. The earlier decision to focus on a single set of criteria for all species was a recognition that life histories, rather than taxonomic affiliation, was the appropriate way to classify species for extinction risk assessment. This meant that different species should enter evaluation using comparable sets of parameters. For example, a 10% decline in abundance would be relatively unimportant for a species with a high reproductive rate if observed at the end of the breeding season, but could be serious for a long-lived, slow-breeding species. Similarly, a continuing decline over several years might be part of the normal life cycle if the mortality affected juveniles, but could be symptomatic of long term continuing decline if breeding adults were the victims and it was seen in a long-lived species. 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' was chosen as a scalar for all time-dependent measures, and 'mature individuals' is used throughout the criteria in place of any measure of overall population size. 'Mature individuals' is defined to measure only the actual breeding size of the population, and will broadly equate to more precise measures of effective population size (N_e). The definitions and usage of these and other terms incorporated into the criteria were much improved through the process of consultation with species experts, but the concern is still often expressed that there cannot be a single criterion that deals with all species. We believe that the approach we have taken is biologically, as well as operationally, the most reasonable, but agree that this depends critically on transforming the information on different species into comparable and relevant statistics by the definition of key terms. These definitions have unfortunately received much less critical review than have the numerical thresholds in the criteria, although to our minds they are more significant.

4. Uncertainty

The rules for application of the new criteria (IUCN, 1994) make it clear that precise information is not required and that the assessor can use expert knowledge along with the best information available to make estimates about current or future trends. Little guidance is given about how this should be done and the responses have inevitably been varied and inconsistent. At one extreme the system has been rejected because of a reluctance to use population size estimates (e.g. the IUCN Cat Specialist Group; (Nowell & Jackson, 1996)). At the other, it has been criticised for simply being based around elaborate guesstimates. However, since the adoption of the criteria, some investigators have developed techniques for dealing with uncertainty in the IUCN classification (Akçakaya *et al.*, in press; Colyvan *et al.*, 1999; Todd & Burgman, 1998). These are now incorporated into a software (Applied Biomathematics, 1999) and we believe they represent a major advance both in standardising and making explicit the way in which uncertainty has been handled.

5. Data deficiency and appropriate categorisation

In practice, deciding whether or not to categorise species as Data Deficient can be difficult. When information on a species is limited the species may only be evaluated against one or two of the criteria. The assessor then has to decide whether this is sufficient to list the species according to these criteria alone or whether it should instead be categorised as Data Deficient. The decision is likely to depend on several things - perhaps most importantly other, circumstantial or inferential, information that the assessor, as a specialist, may have about the species. Collar *et al.* (1994) suggested that where marked habitat loss is suspected, the

assessor is more or less obliged by the precautionary principle to assign threatened status even to very poorly known forms.

The decision as to the adequacy of information depends on attitudes to risk and uncertainty. For example, an extreme precautionary stance would result in any species being listed if there were no evidence that it was secure (i.e. until it had been shown that it met none of the criteria it would be listed as threatened). An extremely risk-prone approach would dictate that all species were assumed to be secure until evidence suggested that they really were at risk - species that had not been shown to meet any of the criteria would be then be listed as Least Concern. The criteria rules suggest adoption of a position at neither of these extremes but that tends towards the precautionary standpoint. Therefore meeting any one criterion necessarily qualifies a species as threatened but meeting none of several criteria may lead to listing as either Lower Risk or Data Deficient.

More recently the development of specific algorithms for deducing Red List status has led to some more specific analyses and recommendations on this point (Akcakaya *et al.*, in press).

6. Low extinction risk and appropriate categorisation

As mentioned above, the terminology and structure of the non-threatened subcategories caused some confusion. The category of Lower Risk is intended for all species that do not meet any of the criteria for Vulnerable and above. Within this category, however, there were two subcategories designed for special cases of Lower Risk. The first of these, Near Threatened, is used for species that only just fail to qualify as threatened. Such cases undoubtedly deserve special attention, but the bounds for classification as Near Threatened are not specified in the IUCN rules. While criteria for Near Threatened would have improved the consistency of use of the subcategory, it became clear that developing robust criteria becomes more difficult as the extinction risk declined, and that there was perhaps more value in retaining the term as a more informal classification. Several assessors have developed their own rules for classifying species into Near Threatened, for example using it where only one of the subcriteria under B or C have been met. In fact, the publication of taxa classified as Near Threatened taxa by IUCN (1996) has helped it to become a significant category and many users have welcomed it for species that they consider worthy of highlighting for various reasons, even if they are not formally listed as threatened.

The other subcategory of Lower Risk, Conservation Dependent, has also provoked much commentary from users. This category has two purposes. By specifically labelling species that are maintained outside the threatened classification by effective conservation actions, such actions are recognised and rewarded. There is less risk that those actions will cease because the species is no longer classified as threatened and the possibility of species vacillating between Vulnerable and Lower Risk is reduced. However, in practice Conservation Dependent has been applied with variable stringency and little consistency. Some assessors have been sparing in its use while others have tended to use it for almost any species where there is ongoing support.

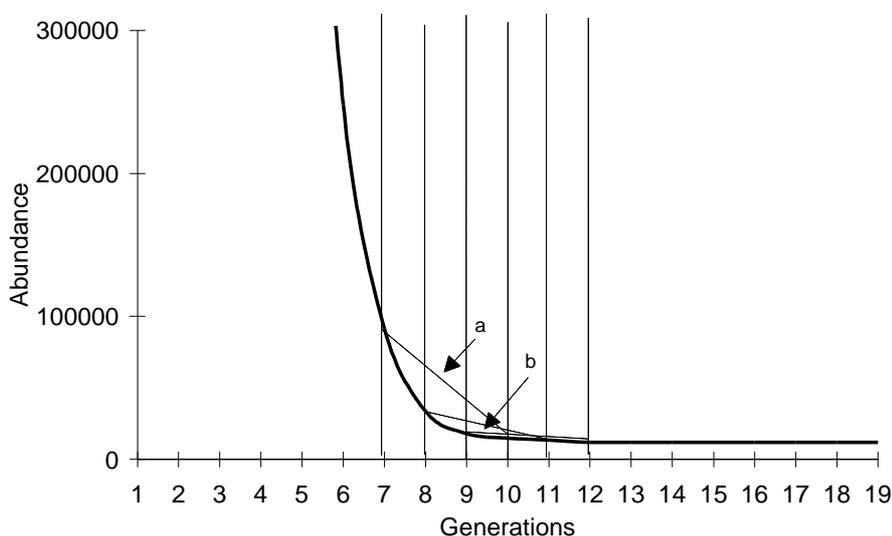
Conservation Dependent also does not sit within the overall scheme as it does not directly measure extinction risk but rather the effectiveness of conservation actions. Thus, species can in theory move straight from Conservation Dependent to Vulnerable, Endangered, Critically Endangered, or even Extinct if the conservation measures were to cease. In practise it reflects another dimension. Additionally, some species will never be Conservation Dependent because the only conservation action is not species specific (e.g. trees).

7. Depleted species

Since the criteria are designed to detect species at risk of extinction they do not identify species that were once numerous but are now depleted. Once a species is stabilised at a level above the threshold values on criteria B and C, and the decline is an historical event, the species will drop off the list. Many species now inhabit only fragments of what was once their geographical range (e.g. Channell & Lomolino, 2000; Lomolino & Channell, 1995) and it is regrettable that it is so easy to forget this. Continuously down-grading of our conservation objectives in line with this shifting baseline is, of course, undesirable (Balmford, 1999) and so it is important to recognise that the criteria do not reflect the general status of biodiversity within a full historical context. The focus on measuring risk of extinction means that continuing to list species that are

still numerous and stable, such as that depicted in Figure 4, cannot be justified. Although many people regret this, and would like to see some explicit notation for depleted species, it is worth drawing the comparison with listing of exploited species. Here, the aim of management is to reduce the population size and then stabilise the population at the new level where productivity is maximised. Managers are hoping that the species will soon reach the point at the right hand side of the figure where they no longer qualify as threatened.

Figure 4. The treatment of depleted species by the criteria. The graph shows a hypothetical species that has gone through a period of rapid decline but that has now stabilised at a new, much reduced level. The new population size is above 10,000 mature individuals means the species will not qualify under criteria B or C, and although it will qualify under criterion A. In this example the species would qualify for Critically Endangered until generation 10 (see the decline rate indicated by line a). The species will then drop down through the threat categories until generation 12 at which point the decline rate drops below the threshold value for Vulnerable (see the decline rate indicated by the line b). Thereafter it no longer qualifies as threatened



8. Regional listing

The criteria were always designed for use at the global level. However, it was recognised that there was also an important demand for criteria to be used at national, local or regional levels. The IUCN system cannot be applied directly at smaller geographical scales without the potential for inaccurate assessments, owing to the fact it then addresses only subsets of entire species or populations or their distributions (Gardenfors, 1996). In addition, there can be counter-intuitive results for priority setting because of the use of threshold values that are relevant to the global scale. In the original rules (IUCN, 1994) some guidance was given and the statement was made that there were problems with regional application. Since then IUCN has been reviewing a set of recommendations for regional applications for the criteria and the latest version of the draft guidelines presents to specific advice to improve their utility at regional scale (Gardenfors *et al.*, 1999).

VII. The IUCN system in use 1996-1999

The new Red List categories have been used widely since their adoption by IUCN in 1994. Most notably they were used in two systematic assessments undertaken by IUCN - the *1996 IUCN Red List of Threatened Animals* (IUCN, 1996) and *the World List of Threatened Trees* (Oldfield, Lusty & MacKinven, 1998). From

these two assessment the overall levels of threat as measured by the criteria can be seen. Altogether, over 15,000 species of animals were assessed and of these 5,205 were recorded as threatened. This is not a fair assessment of the total proportion of the world's species that may be considered threatened with extinction because the assessment is far from comprehensive, and there is no doubt that there is selective assessment of the more highly threatened taxa and regions. However, two major groups were comprehensively reviewed for inclusion in the list - the mammals and the birds. Among mammals, 23% of species are threatened compared with 11% of all birds (Collar *et al.*, 1994) (Table 1). Among taxa that have not been comprehensively assessed, proportions of threatened species are generally higher (Table 1) but since selection of species for assessment is likely to be biased towards the more threatened taxa, it is likely that these are over-estimates of the real values. However, apart from the estimate for trees which is based on a small subset of all trees, the values are not dissimilar to assessments of all native North American species by the Nature Conservancy (TNC, 1996). TNC found the highest threat rates among freshwater invertebrates, fish and amphibians.

Table 1 Summary results of the application of IUCN criteria to various higher taxonomic groupings. The approximate number of species assessed is estimated from IUCN (1996) and Oldfield *et al.* (1998). The figure in parentheses indicates the proportion assessed of the total species diversity on the group. Since assessors may focus on the most threatened species, and on those that are well known, the threat and data deficiency rates may become more unrepresentative as the proportion of species assessed decreases.

Taxon	Approximate number of species assessed (% total)	% threatened of those assessed	% DD of total assessed
Mammals	4763 (100%)	23%	5
Birds	9946 (100%)	11%	1
Reptiles	1480 (20%)	17%	5
Amphibians	600 (12%)	21%	7
Molluscs	>3000 (4%)	31%	18
Trees	10,091 (?0.1%)	59%	4

The frequency with which species were listed as Data Deficient varies with the taxonomic group. Only one percent of birds and five percent of mammals are listed as Data Deficient, reflecting the general level of both scientific and popular interest in these groups. The percentage is higher for less well-studied groups such as the molluscs. The low frequency of Data Deficient listings in the tree assessments is probably attributable to both the selection of taxa for inclusion and the efforts made by the editors to discourage the use of Data Deficient (Oldfield *et al.*, 1998).

All criteria have been used in IUCN assessments although use of the quantitative analysis criterion E is very limited and it has never alone been responsible for a threatened listing (Table 2). Criterion B is the most common criterion used for listing mammal species, followed by the decline criterion (Criterion A). Criterion B is used for many rodents for which range data is more often available than population estimates. Among birds the population size criterion (Criterion C) is most often used with the small range criterion D next. In groups other than birds and mammal there is a stronger emphasis towards one or two criteria. For example, among invertebrates most listings are made using criteria B and D (restricted range areas) and among fishes most listings are made using criteria A and B (declines and restricted areas) (IUCN, 1996).

Table 2: Criteria used in the 1996 IUCN Red List of Threatened Animals (IUCN, 1996) for classifying species into one of the threatened categories (Critically Endangered, Endangered and Vulnerable). The table shows the number of times each criterion was used either solely (Used alone) or in combination with other criteria to determine a species' listing.

Criterion	Mammals		Birds	
	Used alone	Used	Used alone	Used
A	308	434	62	408
B	421	526	45	335
C	92	189	201	769
D	90	150	216	482
E	0	9	0	0

VIII Conclusions

The IUCN Red List criteria were developed over a long period and involved many people from both academic and practical backgrounds. The final formulation of the criteria results from a combination of basic scientific theory and empirical application and testing. It is inevitable that a system such as this that aims to be broad in application will generate some problems in specific cases. However, we feel that an understanding of the principles underlying the system will improve the methods used to apply the system and the interpretation of classifications that result.

IX. Bibliography

- Akcakaya, H. R. & Burgman, M. (1995). PVA in theory and practice. *Conservation Biology* **9**, 705-7.
- Akcakaya, H. R., Ferson, S., Burgman, M. A., Keith, D. A., Mace, G. M. & Todd, C. (in press). Making consistent IUCN classifications under uncertainty. *Conservation Biology*.
- Applied Biomathematics. (1999). RAMAS RedList:Threatened Species Classification Under Uncertainty. Applied Biomathematics, 100 North Country Road, Setauket, NY 11733 USA, Setauket, USA.
- Armbruster, P., Fernando, P. & Lande, R. (1999). Time frames for population viability analysis of species with long generations: an example with Asian elephants. *Animal Conservation* **2**, 69-73.
- Avery, M. I., Gibbons, D. W., Porter, R., Tew, T., Tucker, G. & Williams, G. (1995). Revising the British Red Data List for birds: the biological basis of UK conservation priorities. *Ibis* **137**, 232-239.
- Balmford, A. (1999). (Less and less) great expectations. *Oryx* **33**, 87-88.
- Beddington, J. R. & May, R. M. (1977). Harvesting populations in a randomly fluctuating environment. *Science* **197**, 463-465.
- Beissinger, S. R. & Westphal, M. I. (1998). On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* **62**, 821-841.
- Burgman, M. A., Keith, D. A., Rohlf, F. J. & Todd, C. R. (1999). Probabilistic classification rules for setting conservation priorities. *Biological Conservation* **89**, 227-231.
- Caughley, G. (1994). Directions in conservation biology. *Journal of Animal Ecology* **63**, 215-244.
- Channell, R. & Lomolino, M. V. (2000). Dynamic biogeography and conservation of endangered species. *Nature* **403**, 84-86.
- Collar, N. J. (1998). Extinction by assumption; or, the Romeo Error on Cebu. *Oryx* **32**, 239-244.
- Collar, N. J., Crosby, M. J. & Stattersfield, A. J. (1994). *Birds to Watch 2 - The World List of Threatened Birds*. BirdLife International, Cambridge, UK.
- Collar, N. J., Gonzaga, L. P., Krabbe, N., Nieto, A. M., Naranjo, L. G., III, T. A. P. & Wege, D. C. (1992). *Threatened birds of the Americas. The ICBP/IUCN Red Data Book*. IUCN/ICBP, Cambridge, UK.

- Colyvan, M., Burgman, M. A., Todd, C. R., Akcakaya, H. R. & Boek, C. (1999). The treatment of uncertainty and the structure of the IUCN threatened species categories. *Biological Conservation* **89**, 245-249.
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999). Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* **14**, 405-410.
- Cowling, R. M. & Bond, W. J. (1991). How small can reserves be - an empirical approach in Cape Fynbos, South Africa. *Biological Conservation* **58**, 243-256.
- de Lange, P. J. & Norton, D. A. (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. In *Extinctions* (ed. M. H. Nitecki), pp. 191-246. University of Chicago Press, Chicago.
- Diamond, J. M. (1989). The present, past and future of human-caused extinctions. *Philosophical Transactions of the Royal Society, London, Series B* **325**, 469-477.
- Foufopoulos, J. & Ives, A. R. (1999). Reptile extinctions on land-bridge islands: Life-history attributes and vulnerability to extinction. *American Naturalist* **153**, 1-25.
- Frankham, R. (1995a). 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.
- Franklin, I. R. & Frankham, R. (1998). How large must populations be to retain evolutionary potential? *Animal Conservation* **1**.
- Gaona, P., Ferreras, P. & Delibes, M. (1998). Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). *Ecological Monographs* **68**, 349-370.
- Gardenfors, U. (1996). Application of IUCN Red List categories on a regional scale. In *The 1996 IUCN red List of Threatened Animals* (ed. J. Baillie and B. Groombridge), pp. Intro 63-66. IUCN, Gland.
- Gardenfors, U., Rodriguez, J. P., Hyslop, C., Mace, G. M., Molur, S. & Poss, S. (1999). Draft guidelines for the application of IUCN Red List criteria at regional and national levels. *Species* **31/32**, 58-70.
- 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 and Hall, London.
- Gaston, K. J. & Blackburn, T. M. (1996a). Conservation implications of geographic range size body size relationships. *Conservation Biology* **10**, 638-646.
- Gaston, K. J. & Blackburn, T. M. (1996b). Global scale macroecology: Interactions between population size, geographic range size and body size in the Anseriformes. *Journal of Animal Ecology* **65**, 701-714.
- Gaston, K. J., Blackburn, T. M. & Gregory, R. D. (1999). Does variation in census area confound density estimations? *Journal of Applied Ecology* **36**, 191-204.
- Gaston, K. J. & Chown, S. L. (1999). Geographic range size and speciation. In *Evolution of Biological Diversity* (ed. A. E. Magurran and R. M. May), pp. 236-259. Oxford University Press, Oxford.
- Gaston, K. J. & Lawton, J. H. (1988). Patterns in body size, population dynamics and regional distribution of bracken herbivores. *American Naturalist* **132**, 332-680.
- Gaston, K. J. & McArdle, B. H. (1994). The temporal variability of animal abundances: measures, methods and patterns. *Philosophical Transactions of the Royal Society, London B* **345**, 335-358.
- Gillman, M. P. & Silvertown, J. (1997). Population extinction and IUCN categories: the uncertainty of ecological measurement. In *The role of genetics in conserving small populations* (ed. T. E. Tew, T. J. Crawford, J. W. Spencer, M. B. Usher and J. Warren). JNCC, Peterborough, UK.
- Goodman, D. (1987). The demography of chance extinction. In *Viable populations for conservation* (ed. M. E. Soule), pp. 11-34. Cambridge University Press, Cambridge.
- Hanski, I. (1982). Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* **38**, 210-221.
- Happel, R. E., Noss, J. F. & Marsh, C. W. (1987). Distribution abundance and endangerment of primates. In *Primate Conservation in the Tropical Rain Forest*, vol. 9 (ed. C. W. Marsh and R. A. Mittermeier), pp. 63-82. Alan R. Liss Inc, New York.

- Harcourt, A. (1997). Ecological indicators of risk for primates as judged by species' susceptibility to logging. In *Behavioural ecology and conservation biology* (ed. T. Caro).
- Harcourt, A. H. (1995). Population viability estimates: theory and practice for a wild gorilla population. *Conservation Biology* **9**, 134-142.
- Hedrick, P. W., Lacy, R. C., Allendorf, F. W. & Soule, M. E. (1996). Directions In Conservation Biology Comments On Caughley. *Conservation Biology* **10**, 1312-1320.
- Hedrick, P. W. & Miller, P. S. (1992). Conservation genetics: techniques and fundamentals. *Ecological Applications* **2**, 30-46.
- IUCN. (1990). *1990 IUCN Red List of Threatened Animals*. IUCN, Gland, Switzerland.
- IUCN. (1993). Draft IUCN Red List Categories. IUCN, Gland, Switzerland.
- IUCN. (1994). *IUCN Red List Categories*. IUCN, Gland, Switzerland.
- IUCN. (1996). *The 1996 IUCN Red List of Threatened Animals*. IUCN, Gland, Switzerland.
- Karr, J. R. (1982). Population variability and extinction in the avifauna of a tropical land bridge island. *Ecology* **63**, 1975-1978.
- 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.
- Kokko, H. & Ebenhard, T. (1996). Measuring the strength of demographic stochasticity. *J. theoretical biology* **183**, 169-178.
- Kunin, W. E. & Gaston, K. J. (1993). The biology of rarity: patterns, causes and consequences. *TREE* **8**, 298-301.
- Kuzmin, S. L., Pavolv, D. S., Stepanyan, L. S., Rozhnov, V. V. & Mazin, L. N. (1998). The state of and perspectives for the IUCN Red List of Animals. *Russian Journal of Zoology* **2**, 539-546.
- Lande, R. (1993a). Risks Of Population Extinction From Demographic and Environmental Stochasticity and Random Catastrophes. - *American Naturalist* - **142**, - 911-927.
- Lande, R. (1998). Anthropogenic, ecological and genetic factors in extinction. In *Conservation in a Changing World* (ed. G. M. Mace, A. Balmford and J. R. Ginsberg). Cambridge University Press, Cambridge.
- Lande, R. C. (1993b). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**, 911-927.
- Lawton, J. H. (1995). Population dynamic principles. In *Extinction Rates* (ed. J. H. Lawton and R. M. May). OUP, Oxford UK.
- Leader-Williams, N., Albon, S. D. & Berry, P. S. M. (1990). Illegal exploitation of black rhinoceros and elephant populations: patterns of decline, law enforcement and patrol effort in Luangwa Valley, Zambia. *J. Appl. Ecol.* **27**, 1055-1087.
- Legendre, S., Clobert, J., Moller, A. P. & Sorci, G. (1999). Demographic stochasticity and social mating system in the process of extinction of small populations: The case of passerines introduced to New Zealand. *American Naturalist* **153**, 449-463.
- Lindenmayer, D. B., Clark, T. W., Lacy, R. C. & Thomas, V. C. (1993). Population Viability Analysis As a Tool in Wildlife Conservation Policy - With Reference to Australia. *Environmental Management* **17**, 745-758.
- Lomolino, M. V. & Channell, R. (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. & Lande, R. (1998). The critical effective size for a genetically secure population. *Animal Conservation* **1**, 70-72.
- Mace, G. M. (1995). Classification of threatened species and its role in conservation planning. In *Extinction Rates* (ed. J. H. Lawton and R. M. May), pp. 197-213. Oxford University Press, Oxford.
- Mace, G. M., Collar, N., Cooke, J., Gaston, K., Ginsberg, G., Leader-Williams, N., Maunder, M. & Milner-Gulland, E. J. (1992). The development of new criteria for listing species on the IUCN Red List. *Species* **19**, 16-22.
- Mace, G. M. & Hudson, E. J. (1999). Attitudes toward sustainability and extinction. *Conservation Biology* **13**, 242-246.
- Mace, G. M. & Lande, R. (1991). Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conserv. Biol.* **5**, 148-157.
- Mace, G. M. & Stuart, S. N. (1994). Draft IUCN Red List Categories. *Species* **21/22**, 13-24.

- MacPhee, R. D. M. & Flemming, C. (1999). Requiem aeternam: the last five hundred years of mammalian species extinctions. In *Extinctions in near time* (ed. R. D. M. MacPhee). Kluwer Academic/Plenum Publishers, New York.
- Mangel, M. & Tier, C. (1994). Four facts every conservation biologist should know about persistence. *Ecology* **75**, 607-614.
- Matsuda, H., Takenaka, Y., Yahara, T. & Uozumi, Y. (1998). Extinction risk assessment of declining wild populations: The case of the southern bluefin tuna. *Researches On Population Ecology* **40**, 271-278.
- Matsuda, H., Yahara, T. & Uozumi, Y. (1997). Is tuna critically endangered? Extinction risk of a large and overexploited population. *Ecological Research* **12**, 345-356.
- Maurer, B. A. (1994). *Geographical population analysis: tools for the analysis of biodiversity*. Blackwell Scientific, Oxford, UK.
- May, R. M., Lawton, J. H. & Stork, N. E. (1995). Assessing extinction rates. In *Extinction Rates* (ed. J. H. Lawton and R. M. May), pp. 1-24. Oxford University Press, Oxford.
- McArdle, B. H., Gaston, K. J. & Lawton, J. H. (1990). Variation in the size of animal populations: patterns, problems and artefacts. *Journal of Animal Ecology* **59**.
- Millsap, B. A., Gore, J. A., Runde, D. A. & Cerulean, S. I. (1990). Setting priorities for the conservation of fish and wildlife species in Florida. *Wildlife Monographs* **111**, 1-57.
- Milner-Gulland, E. J. & Beddington, J. (1993). The exploitation of the elephant for the ivory trade - an historical perspective. *Proceedings of the Royal Society of London, Series B* **252**, 29-37.
- Milner-Gulland, E. J. & Mace, R. (1998). *Conservation of Biological Resources*. Blackwell Science, Oxford, UK.
- Molloy, J. & Davis, A. (1992). *Setting priorities for the conservation of New Zealand's threatened plants and animals*. Department of Conservation, Wellington, New Zealand.
- Munton, P. (1987). Concepts of threat to the survival of species used in Red Data Books and similar compilations. In *The Road to Extinction* (ed. R. Fitter and M. Fitter), pp. 71-111. IUCN, Gland, Switzerland.
- Musick, J. A. (in press). Criteria to define extinction risk in marine fishes. The American Fisheries Society Initiative. *Fisheries* .
- Myers, R. A., Barrowman, N. J., Hutchings, J. A. & Rosenberg, A. A. (1995). Population dynamics of exploited fish stocks at low population levels. *Science* **269**, 1106-1108.
- Newmark, W. D. (1991). Tropical Forest Fragmentation and the Local Extinction Of Understory Birds In the Eastern Usambara Mountains, Tanzania. - *Conservation Biology* - **5**, - 67-78.
- Nowell, K. & Jackson, P. (1996). Wild cats; status survey and conservation action plan. IUCN, Gland, Switzerland.
- Oldfield, S., Lusty, C. & MacKinven, A. (1998). The world list of threatened trees. World Conservation Press, Cambridge.
- Pimm, S. L. (1992). *The Balance of Nature*. University of Chicago Press, Chicago.
- Pimm, S. L., Jones, H. L. & Diamond, J. M. (1988). On the risk of extinction. *Amer. Nat.* **132**, 757-785.
- Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. (1995). The future of biodiversity. *Science* **269**, 347-350.
- Purvis, A., Gittleman, J. L., Cowlshaw, G. C. & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society of London, series B* .
- Richter-Dyn, N. & Goel, N. S. (1972). On the extinction of a colonising species. *Theoretical Population Biology* **3**, 406-433.
- Seal, U. S., Foose, T. J. & Ellis-Joseph, S. (1994). Conservation assessment and management plans (CAMPs) and global captive action plans (GCAPs). In *Creative Conservation - the Interactive Management of Wild and Captive Animals* (ed. P. J. Olney, G. M. Mace and A. T. C. Feistner), pp. 312-325. Chapman & Hall, London.
- Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters*. MacMillan, New York.
- 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. In *Patterns and processes in the history of life* (ed. D. M. Raup and D. Jablonski), pp. 259-276. Springer Verlag, Berlin.
- Simberloff, D. & Gotelli, N. (1984). Effects Of Insularization On Plant Species Richness In the Prairie Forest Ecotone. - *Biological Conservation* - **29**, - 27-46.
- Sorci, G., Moller, A. P. & Clobert, J. (1998). Plumage dichromatism of birds predicts introduction success in New Zealand. *Journal of Animal Ecology* **67**, 263-269.

- Soule, M. E. (1980). Thresholds for survival: maintaining fitness and evolutionary potential. In *Conservation biology: an evolutionary-ecological perspective* (ed. M. E. Soule and B. A. Wilcox), pp. 151-169. Sinauer Associates, Sunderland, Mass.
- Sutherland, W. J. (1996). *Ecological census techniques*. Cambridge University Press, Cambridge, UK.
- Taylor, B. L. (1995). The reliability of using population viability analysis for risk classification of species. *Conservation Biology* **9**, 551-558.
- Taylor, B. L. & Gerrodette, T. (1993). The uses of statistical power in conservation biology: the vaquita and the spotted owl. *Conservation Biology* **7**, 489-500.
- Terborgh, J. & Winter, B. (1980). Some causes of extinction. In *Conservation Biology: an evolutionary-ecological perspective* (ed. M. E. Soule and B. A. Wilcox), pp. 119-133. Sinauer Associates, Sunderland, Mass.
- Thomas, C. D. & Mallorie, H. C. (1985). Rarity, species richness and conservation: butterflies of the Atlas Mountains in Morocco. *Biological Conservation* **33**, 95-117.
- TNC. (1996). Priorities for conservation: 1996 annual report card for US plant and animal species. The Nature Conservancy, Arlington, VA.
- Todd, C. R. & Burgman, M. A. (1998). Assessment of threat and conservation priorities under realistic levels of uncertainty and reliability. *Conservation Biology* **12**, 966-974.
- Usher, M. B. (1991). Scientific requirements of a monitoring programme. In *Monitoring for Conservation and Ecology* (ed. F. B. Goldsmith), pp. 15-32. Chapman and Hall, London.
- Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. (1991). What to protect? -systematics and the agony of choice. *Biological Conservation* **55**.
- Warren, M. S., Barnett, L. K., Gibbons, D. W. & Avery, M. I. (1997). Assessing national conservation priorities: An improved Red List of British butterflies. *Biological Conservation* **82**, 317-328.
- Woodroffe, R. & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126-2128.

GEORGINA M. MACE
 Institute of Zoology,
 Zoological Society of London,
 Regent's Park,
 London NW1 4RY.
 Email: Georgina.Mace@ioz.ac.uk.