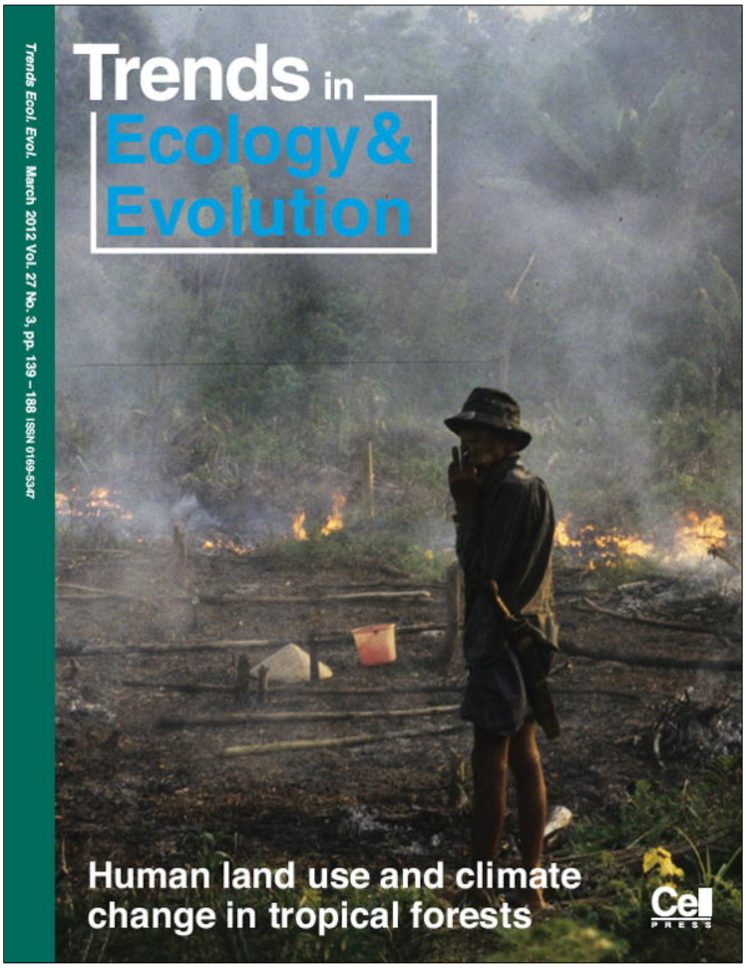
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Are comparative studies of extinction risk useful for conservation?

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Large-scale, comparative studies of species extinction risk have become common in conservation science, but their influence on conservation practice appears limited. The link between such studies and the practice of conservation breaks down in two key places. First, results of comparative studies are often ambiguous, inconsistent and difficult to translate into policy. Second, conservation as currently practiced emphasizes the rescue and protection of currently threatened biodiversity, whereas comparative studies are often better suited to a proactive approach that anticipates and prevents future species declines. Scientists should make their research more accessible by addressing the first issue. Policy-makers and managers, in turn, could make better use of comparative studies by moving towards more preventative approaches to conservation planning.

Desktop studies of extinction risk

Most people involved in conservation would agree that conservation practice should be underpinned by good science. Science should provide conservation workers with an understanding of the species, community or ecosystem they work on, and a broader context of ecological theory within which to place their system. Thus, science should play a strong role in conservation policy and planning by providing baseline data on the status of the biodiversity of a region, elucidating cause–effect relationships between interventions and conservation outcomes, or identifying general principles for allocating funds to projects of high priority. Unfortunately, links between research and conservation practice often break down (e.g. [1,2]). It seems to us that this separation between science and practice is more probable the further the research is removed from real-world conservation problems, and the socio-economic and political systems within which conservation must operate. Hence, desktop-based studies that are often more academic or esoteric in nature will be more prone to disconnection from conservation practice compared with field-based research with a narrow focus on specific conservation issues and more direct feedback regarding its impact on conservation practice.

In this article, we examine the influence on conservation practice of a particular kind of desktop-based conservation science that has become increasingly popular in recent years: systematic comparative studies of species extinction risk, especially those using a phylogenetic analysis framework [3]. These studies involve the analysis of large, multispecies, synthetic data sets compiled from published literature or other public sources. The broad aims of such studies are to discover and describe generalizations about patterns and processes in the decline or threat status of species. This 'big-picture' approach to conservation science seems to have emerged as part of a more general rise in popularity of large-scale, comparative analyses in ecology since the 1980s, typified by the field of macroecology [4].

The comparative extinction risk literature is now substantial and growing rapidly. For this reason, and because invariably the rationale is their importance for conservation, we feel that it is timely to examine whether these studies are making a tangible contribution to conservation practice. To assess this, we ask the following questions: (i) what do these studies promise (i.e. what are the aims or intended outcomes)? (ii) Do they deliver the promised outcomes? (iii) Do the outcomes match the scientific needs of conservation? (iv) Can the outcomes be translated easily into conservation policy and practice? (v) Is there evidence that the outcomes are being adopted into policy and practice? And (vi) If not, where does the link between science and practice fail, and can the two be reconciled?

What do comparative extinction risk studies promise?

The aims and outcomes of comparative extinction risk studies can be divided into three basic categories: (i) Call to action: these are studies that document and describe the magnitude or severity of the extinction crisis. For example, Ceballos and Ehrlich [5] showed that mammal extinctions at the population level have been far more widespread than expected from the number of species-level extinctions, and they urged conservation managers to give population and species losses equal prominence. (ii) Prioritizing species: these studies describe the taxonomic, phylogenetic or biological selectivity of extinction risk, without necessarily identifying the processes driving this selectivity. For example, Cardillo and Bromham [6] identified families of Australian mammals with more threatened species than expected under a null model. The implication of such studies, often implicit or only vaguely alluded to, is that this selectivity should be used as a basis for prioritizing species in the allocation of conservation funds, based on their membership of a 'high-risk' group (i.e. a group

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statistically more likely to contain threatened species). (iii) Identifying threatening processes: these studies identify the factors that correlate with extinction risk across species, and use these correlations to infer the processes driving species decline. Often, the threatening processes are already known to be one or more of the 'evil quartet' of habitat destruction, overexploitation, introduced species and secondary extinction [7]. However, comparative studies promise to reveal the relative importance of different threat types, and how they interact with biological traits to elevate extinction risk. For example, Owens and Bennett [8] showed that, among bird families, habitat specialists are more likely to be threatened by habitat loss, whereas large-bodied species are more likely to be threatened by overexploitation.

In contrast to population viability analyses, which are usually specific to a single study population and cannot be generalized [9,10], the comparative approach steps back from the idiosyncrasies of particular systems to identify general patterns of extinction risk across large sets of species. This allows the following question to be asked: why do species differ in their current risk of extinction? An obvious answer would appear to be that species differ in where they live and, thus, in the threats that they are exposed to. However, there are some cases where closely related species that inhabit the same region differ widely in extinction risk; for example the jerboas (*Allactaga* spp.) of southwestern Asia [11]. In these cases, the differences might lie in the biology of the species (e.g. some species may have larger litters or shorter generations), and comparative statistical models are needed to tease apart the potentially large number of interacting biological and external factors contributing to threat status. Such models promise to improve understanding of the driving forces of species decline. They also present the possibility of predicting the potential threat status of a species from its biology, thereby allowing planners to anticipate possible future declines, and take preventative measures [12–17].

Do comparative extinction risk studies deliver their promises?

Studies falling into the 'call to action' category have probably succeeded in raising awareness of the magnitude of the extinction crisis and highlighting the urgency with which action is needed. This is particularly true for studies published in high-impact journals, which are often accompanied by media releases and gain worldwide media attention. For example, a paper by Thomas *et al*. [18] that predicted hundreds of extinctions owing to habitat shifts associated with global warming was widely reported in the mainstream media and on the internet [19], and no doubt contributed to a greater general awareness of the potential impact of global warming on natural communities. Although those already involved in conservation policy development might need little convincing of the seriousness of the extinction crisis, 'call to action' studies might help them to put forward a stronger case to funding agencies.

Is there a better understanding of patterns of selectivity of extinction risk, or the relative importance of different threatening processes to different kinds of species, as a result of comparative studies? The answer must be yes, although whether this improved understanding has spread widely among conservation practitioners and policy developers, or is still confined to the academic conservation biology community, is less clear. One thing that is known from such studies is that responses to human impacts by different taxa in different regions are, to a large extent, idiosyncratic: there do not seem to be many general, prescriptive indicators of high extinction risk potential [20,21]. Perhaps the nearest one can get to generalizations is to note that some biological correlates of extinction risk crop up more frequently than others. In mammals, amphibians and birds, for example, small geographic range size is often associated with rapid rates of population decline [16,20,22].

It seems fair to conclude that comparative extinction risk studies have met the three 'proximate' aims that we outlined above. The next question is whether the outcomes of comparative studies match the needs of conservation, and whether comparative studies achieve their 'ultimate' aim of changing human behavior and influencing conservation policy and practice.

Do the aims or outcomes of comparative extinction risk studies match the scientific needs of conservation?

Identifying what practical conservation needs from science is not straightforward, but two recent papers by Sutherland and colleagues present the results of a systematic attempt to identify the most important scientific questions for conservation, for the UK [23] and globally [24]. Comparative extinction risk studies are relevant to very few of these questions (Box 1). For the UK exercise, our subjective judgment is that seven of the 100 questions could be addressed using a comparative approach to analyzing patterns of extinction risk. For the global exercise, we judge that the comparative approach is relevant to only three questions. Even under the category of 'species management', there are no questions for which the comparative approach seems relevant. If these two papers are a reasonable reflection of the science being requested by conservation practice, then the comparative approach has, at best, a minor role to play in meeting the scientific needs of conservation.

Can the outcomes of comparative studies be translated easily into conservation policy or practice?

Notwithstanding the mismatch between the mainstream scientific needs of conservation and the outcomes of comparative extinction risk studies, it is useful to explore how easily these outcomes might be applied to real-world conservation problems. One application of comparative studies is to provide the basis for some form of species-based prioritization. Given the scarcity of funds available for conservation, prioritization of funds towards particular species or areas is becoming increasingly systematic and quantitative [25]. Apart from the prioritization algorithms themselves, the principal contribution made by science to systematic conservation planning is to provide the baseline data needed to assess the current threat status of species [e.g. International Union for Conservation of Nature (IUCN) Red List [11]], or to identify threatened ecosystems or habitat types. Many conservation agencies simply prioritize species formally listed as threatened, so that prioritization is based

Box 1. 200 scientific questions important to conservation

Sutherland and colleagues [23,24] compiled the 100 scientific questions (for the UK and the world, respectively) that if answered, would have the greatest impact on conservation of biodiversity. These sets of questions were arrived at by whittling down much larger sets of candidate questions through a series of questionnaires and workshops attended by conservation scientists, planners and practitioners. We judge that of these 200 questions, the following are ones for which comparative, desktop-based analyses of extinction risk could provide useful answers. The wording of some questions has been modified for brevity.

UK

- Why have many woodland birds declined?
- Which ecological principles should guide the choice of species appropriate for hunting?
- Which species are the best indicators of the effects of climate change on communities?
- Which habitats and species might be lost completely because of climate change?
- What is the relationship between climate change and patterns of species extinction?
- How does climate change interact with other ecological pressures?
- Are there reliable ways to predict the sustainability of poorly known species using life-history and other ecological characteristics?

World

- Which elements of biodiversity are most vulnerable to climate change?
- How will human responses to climate change affect biodiversity?
- Which aquatic species and communities are most vulnerable to human impacts?

Roughly speaking then, comparative extinction risk studies might help answer 5% of the questions being asked by conservationists (i.e. 10 questions out of 200). Does this offer some guide to the proportion of conservation science funding that might reasonably be allocated to comparative studies?

mostly on what baseline data inform about the current status of species.

Comparative studies, by contrast, offer a more predictive approach, based on statistical generalizations. So a species might be selected for a priority list based on its membership of a group that is statistically highly likely to contain threatened species. This group can be taxonomic (e.g. the marsupial family Potoroidea [6]), or it can be defined morphologically (e.g. large-bodied marine fishes [26]) or geographically (e.g. island-dwelling microbats [27]). In this way, such statistical generalizations could provide additional evidence for assessing the current status of species for which direct data on population trends or geographic distribution are lacking [26]. Alternatively, modeled extinction risk could help identify currently unthreatened species that might have greater potential to become threatened in the future based on their suite of biological traits [13–16,27,28]. This would represent a more proactive, anticipatory approach to species prioritization than is commonly practiced [12].

Is there evidence that outcomes of comparative studies have been adopted into conservation policy or practice?

It is difficult to judge properly the global uptake of comparative extinction risk studies without an extensive perusal of policy documents from conservation agencies the world over. Instead, we examined as case studies species action plans and policy statements relevant to threatened species and biodiversity, for the two countries in which we work, Australia and Indonesia. This included documents from each of the seven State and Commonwealth departments of Australia responsible for environmental management ([29–34] and websites detailed in Box 2), and the Indonesian Biodiversity Strategy and Action Plan 2003–2020 [35] and four species-specific action plans [36–39].

Conservation planning in the Australian departments seems to emphasize area-based rather than species-based prioritization. Nonetheless, each department has an explicit strategy for prioritizing species for conservation: these vary in detail, but are usually based on listing species as threatened or classifying species by their level of extinction risk. The criteria for listing species as threatened are based primarily on direct estimates of remaining population size, geographic distribution size, rates of decline or degree of population fragmentation. There is no evidence that any kind of statistical generalizations are used in the listing processes, in the sense that the membership of a species of a group identified as particularly vulnerable forms part of the formal justification for listing.

Yet there are hints that the kind of predictive approach permitted by comparative extinction risk studies is at least in the minds of the scientific committees that formulate threatened species policies in Australia. For example, it is common for mammal action plans, recovery plans or listing advice to mention that a species lies within the 'critical weight range' (CWR). This refers to the observation that most Australian mammal species that have gone extinct or declined severely since European occupation have been within an intermediate weight range of 35 g to 5.5 kg, perhaps because this matches the preferred prey sizes of introduced predators [40]. The implication is that mammal species within the CWR are inherently at greater risk of

Box 2. Website-based species action plans and policy statements from Australia

Below is a list of website-based species action plans and policy statements that are relevant to threatened species and biodiversity, published by the Australian State and Commonwealth departments that are responsible for environmental management.

- Australian Government Department of Sustainability, Environment, Water, Population and Communities: *Action Plans and Conservation Overviews* (http://www.environment.gov.au/biodiversity/threatened/publications/action/index.html).
- Australian Government Department of Sustainability, Environment, Water, Population and Communities: *EPBC Act Policy Statements* (http://www.environment.gov.au/epbc/guidelines-policies.html).
- NSW Government, Office of Environment and Heritage: *Criteria for Listing Threatened Species* (http://www.environment.nsw.gov.au/threatenedspecies/listingts.htm).
- Queensland Government Department of Environment & Resource Management: *Back on Track Species Prioritization Framework* (http://www.derm.qld.gov.au/wildlife-ecosystems/wildlife/back_on_track_species_prioritisation_framework/index.html).
- Queensland Government Department of Environment & Resource Management: *Threatened Species* (http://www.derm.qld.gov.au/wildlife-ecosystems/wildlife/threatened_plants_and_animals/index.html).

extinction, so there is a need to monitor them. CWR status is never an explicit criterion for threat listing, but it does seem to be used to add weight to the arguments presented to justify assigning a species to a high-priority group.

Other statements from the Australian policy documents also suggest that statistical generalizations about extinction risk carry at least some weight. A Victorian document states that 'species most at risk include those that have low ecological tolerances, low genetic variation, long generation times, specialised requirements, poor dispersal and a narrow geographic range' [33]. These are exactly the kind of generalizations that comparative extinction risk studies seek to test and clarify, but there are no scientific references cited to support this statement, and we wonder whether the statement is based on actual results of any explicit, published comparative tests. Again however, the generalizations asserted here do not appear to play a formal role in setting the policy agenda; rather they form part of the supporting background information.

Evidence for the influence of species-group generalizations was less evident in the Indonesian documents. The Indonesian National Biodiversity Action Plan [35] focuses on strategies to strengthen the capacity of the country to identify and address the most urgent conservation problems. No references are made to predictive studies of species extinction, and threats to species are discussed only in relation to their status in the IUCN Red List. Indonesia is in the process of developing conservation action plans for its most iconic threatened species, initially mostly large mammals. Selection methods for these species are not specified apart from their IUCN Red Listing, which does not use any predictive inferences based on comparative studies. However, the international public appeal of large mammals such as the Sumatran tiger and orangutan probably plays a role.

Where does the link between the science and the practice fail, and can the two be reconciled?

At least in Australia and Indonesia, there is little evidence that conservation policy, planning or practice have been influenced in any substantial way by the comparative extinction risk literature. If 'importance to conservation' is the overarching rationale for these kinds of study, then this must be seen as a failure of communication between scientists and practitioners. We can identify two key points at which the link between the science and the practice fails.

First is a mismatch between what comparative studies provide and what conservation needs. If we consider the '100 questions' exercise as a reasonable approximation of what conservation needs from science, then the big-picture, statistical patterns provided by comparative studies are relevant to only a small set of issues at the fringes of mainstream conservation. This probably reflects, at least partly, the prevailing mindset of conservation as a reactive, crisis discipline, whereas the outcomes of comparative studies are more suited to a proactive, predictive approach that emphasizes the anticipation and prevention of species declines. Yet there does seem to be some need among conservation planners for information that would permit them to adopt a more proactive approach. For example, a South Australian document states that 'Other species and communities are declining at rapid rates but do not yet meet state and national criteria for listing as threatened. Identifying and managing these species before they decline to critical levels is a priority. For other species we have insufficient information to demonstrate that they fall into a threatened species category but because of our knowledge of threats we have reason to believe that they could be listed as threatened' [31]. Comparative extinction risk models offer the potential to meet these needs, by providing the basis for a provisional assignment of species to categories of extinction risk using information on biology, geography and phylogeny.

The other principal reason that comparative studies fail to transmit to conservation practice is that there are few clear messages that have emerged from this body of science. In our opinion, results of comparative extinction risk studies are often vague, inconsistent, complex and clouded by uncertainty. In some cases, different studies reach different conclusions: for example, the existence of a 'CWR' for Australian mammals has been called into question [6] as well as supported [41]. This does not offer a robust guide for developing policy.

Nonetheless, we are optimistic that comparative studies of extinction risk can become more relevant to conservation practice. We recommend the following as steps towards reducing the mismatch between the outcomes of comparative studies and the needs of conservation:

First, researchers should adopt a somewhat 'smaller picture' view by restricting the geographic and taxonomic scope of comparative analyses, and aiming for clearer, more focused outcomes on particular hypotheses. For example, Johnson and Isaac [41] showed that the CWR seems to apply within some geographic and ecological subsets of Australian mammals, but not others, whereas Olden *et al.* [42] showed that life-history traits had a high degree of power to predict extinction risk of fish species in the Lower Colorado River Basin in the USA. Identifying relatively small groups of species with elevated risk potential within restricted geographic areas might increase the likelihood of recommendations being translated into preventative action.

Second, researchers should value-add comparative extinction risk models by using them to provide recommendations that are more clearly interpretable in conservation terms; for example, including predicted extinction risk in area prioritization algorithms, or provisionally assigning data-deficient species to threat categories.

Third, conservation policy developers should do more to accommodate a proactive, predictive approach to conservation planning that seeks to identify species potentially at risk, rather than focus solely on rescuing species currently at risk. This would be particularly useful in areas such as the Bornean rainforests, where resource exploitation pressure is heavy but baseline taxonomic or ecological data are scarce.

Finally, and perhaps most importantly, scientists carrying out comparative extinction risk studies should rethink their expectations that their research will be of immediate, practical value for conservation. They should consider their work as primarily an academic exercise that contributes to a general, diffuse accumulation of knowledge about the ecology of decline and extinction under global change, some of which might filter through to conservation practice. They should accept that this is a perfectly legitimate scientific pursuit as long as this kind of research is funded mostly through academic channels and does not divert a disproportionate share of funding (Box 1) away from projects of more direct practical conservation value.

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References
1 Meijaard, E. and Sheil, D. (2007) Is wildlife research useful for wildlife conservation in the tropics? A review for Borneo with global implications. *Biodivers. Conserv.* 16, 3053–3065
2 Sutherland, W.J *et al.* (2004) The need for evidence-based conservation. *Trends Ecol. Evol.* 19, 305–308
3 Fisher, D.O. and Owens, I.P.F. (2004) The comparative method in conservation biology. *Trends Ecol. Evol.* 19, 391–398
4 Brown, J.H. (1995) *Macroecology*, University of Chicago Press
5 Ceballos, G. and Ehrlich, P.R. (2002) Mammal population losses and the extinction crisis. *Science* 296, 904–907
6 Cardillo, M. and Bromham, L. (2001) Body size and risk of extinction in Australian mammals. *Conserv. Biol.* 15, 1435–1440
7 Diamond, J.M. (1989) Overview of recent extinctions. In *Conservation for the Twenty-first Century* (Weston, D. and Pearl, M.C., eds), pp. 37–41, Oxford University Press
8 Owens, I.P.F. and Bennett, P.M. (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl. Acad. Sci. U.S.A.* 97, 12144–12148
9 Soule, M.E., ed. (1987) *Viable Populations for Conservation*, Cambridge University Press
10 Caughley, G. (1994) Directions in conservation biology. *J. Anim. Ecol.* 63, 215–244
11 IUCN (2009) *2009 IUCN Red List of Threatened Species*, IUCN
12 Cardillo, M. (2006) Disappearing forests and biodiversity loss: which areas should we protect? *Int. Forest. Rev.* 8, 251–255
13 Cardillo, M. *et al.* (2006) Latent extinction risk and the future battlegrounds of mammal conservation. *Proc. Natl. Acad. Sci. U.S.A.* 103, 4157–4161
14 Cardillo, M. *et al.* (2004) Human population density and extinction risk in the world's carnivores. *PloS Biol.* 2, 909–914
15 Larson, E.R. and Olden, J.D. (2010) Latent extinction and invasion risk of crayfishes in the southeastern United States. *Conserv. Biol.* 24, 1099–1110
16 Lee, T.M. and Jetz, W. (2011) Unravelling the structure of species extinction risk for predictive conservation science. *Proc. R. Soc. B: Biol. Sci.* 278, 1329–1338
17 Meijaard, E. *et al.* (2008) Phylogenetic age is positively correlated with sensitivity to timber harvest in Bornean mammals. *Biotropica* 40, 76–85
18 Thomas, C.D. *et al.* (2004) Extinction risk from climate change. *Nature* 427, 145–148
19 Ladle, R.J. *et al.* (2005) Scientists and the media: the struggle for legitimacy in climate change and conservation science. *Interdisciplinary Sci. Rev.* 30, 231–240
20 Cardillo, M. *et al.* (2008) The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. B: Biol. Sci.* 275, 1441–1448
21 Mace, G.M. *et al.* (2010) Population and geographic range dynamics: implications for conservation planning. *Philos. Trans. R. Soc. B: Biol. Sci.* 365, 3743–3751
22 Cooper, N. *et al.* (2008) Macroecology and extinction risk correlates of frogs. *Global Ecol. Biogeogr.* 17, 211–221
23 Sutherland, W.J. *et al.* (2006) The identification of 100 ecological questions of high policy relevance in the UK. *J. Appl. Ecol.* 43, 617–627
24 Sutherland, W.J. *et al.* (2009) One hundred questions of importance to the conservation of global biological diversity. *Conserv. Biol.* 23, 557–567
25 Margules, C.R. and Pressey, R.L. (2000) Systematic conservation planning. *Nature* 405, 243–253
26 Reynolds, J.D. *et al.* (2005) Biology of extinction risk in marine fishes. *Proc. R. Soc. Lond Ser. B: Biol. Sci.* 272, 2337–2344
27 Jones, K.E. *et al.* (2003) Biological correlates of extinction risk in bats. *Am. Nat.* 161, 601–614
28 Purvis, A. *et al.* (2000) Predicting extinction risk in declining species. *Proc. R. Soc. Lond. Ser. B: Biol. Sci.* 267, 1947–1952
29 NSW Department of Environment & Climate Change (2008) *New South Wales Parks Network Establishment Plan 2008*, Department of Environment & Climate Change NSW
30 NSW Government Department of Environment and Heritage (2007) *Threatened Species Assessment Guidelines: The Assessment of Significance*, NSW Government Department of Environment and Heritage
31 Department for Environment & Heritage (2007) *No Species Loss: A Nature Conservation Strategy for South Australia 2007–2017*, Government of South Australia
32 Threatened Species Section (2010) *Prioritization of Threatened Flora and Fauna Recovery Actions for the Tasmanian NRM Regions*, Tasmanian Department of Primary Industries, Parks, Water and Environment
33 Victorian Government Department of Sustainability & Environment (2010) *Victoria's Biodiversity Strategy 2010–2015 Consultation Draft*, Victorian Government Department of Sustainability & Environment
34 CALM (1994) *Setting Priorities for the Conservation of Western Australia's Flora and Fauna*, Department of Conservation & Land Management
35 BAPPENAS (2003) *Indonesian Biodiversity Strategy and Action Plan. National Document*, National Development Planning Agency (BAPPENAS)
36 Indonesian Ministry of Forestry (2007) *Strategy and Action Plan for the Conservation of Rhinos in Indonesia 2007–2017*, Indonesian Ministry of Forestry
37 Indonesian Ministry of Forestry (2007) *Strategi dan rencana aksi konservasi orangutan Indonesia 2007–2017*, Indonesian Ministry of Forestry
38 Indonesian Ministry of Forestry (2007) *Sumatran Tiger Conservation Strategy and Action Plan. Strategi dan Rencana Aksi Konservasi Harimau Sumatera*, Indonesian Ministry of Forestry
39 Soehartono, T. *et al.* (2007) *Strategi Dan Rencana Aksi Konservasi Gajah Sumatera Dan Gajah Kalimantan 2007–2017*, Indonesian Ministry of Forestry
40 Burbidge, A.A. and McKenzie, N.L. (1989) Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biol. Conserv.* 50, 143–198
41 Johnson, C.N. and Isaac, J.L. (2009) Body mass and extinction risk in Australian marsupials: the 'Critical Weight Range' revisited. *Aust. Ecol.* 34, 35–40
42 Olden, J.D. *et al.* (2008) Trait synergisms and the rarity, extirpation and extinction risk of desert fishes. *Ecology* 89, 847–856