LETTER

Spatial scale and the conservation of threatened species

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Abstract

The spatial scale of conservation necessary to avoid species extinctions is one of the most vigorous debates in conservation biology. One approach holds that protecting sites should be the primary level for action on the ground, the other that conservation action targeting broader seascapes and landscapes is more important. We address this debate systematically by assessing the appropriate spatial scales of conservation for all 4,239 threatened mammals, birds, tortoises and turtles, and amphibians. We find that, in the short- to medium term, 20% of these species are dependent on conservation at single sites, 62% on multiple sites, 18% on both sites and sea- or landscape-scale efforts, and <1% on broad-scale actions alone (where sites are variably sized units that are actually or could potentially be managed for conservation, and "broad scale" refers to sea- or landscape-scale and is determined by the needs of the species in question). Calls for broad-scale conservation action have generally focused on terrestrial birds and mammals, and we confirm that a fifth and a tenth of these, respectively, require conservation action at the landscape scale. However, we also find that two-fifths of threatened freshwater turtles and one-fifth of threatened amphibians depend on broad-scale conservation action to address changes in freshwater processes. Furthermore, the overwhelming majority of threatened marine mammals, birds, and turtles require urgent conservation action at the seascape scale. Our key conclusion is that neither site-scale nor broad-scale approaches alone can prevent mass extinction. Although site protection should remain the cornerstone for almost all threatened species, we demonstrate that a substantial proportion and unexpected diversity of threatened species will be lost in the absence of urgent conservation interventions at the sea- or landscape scale.

Introduction

The debate on the appropriate spatial scale of conservation action dates to the first applications of island biogeography to the design of nature reserves and the recognition that some species require large areas to maintain viable populations (Terborgh 1974; Diamond 1975). A growing body of evidence indicates that species that occur at low densities, have sizeable home ranges, are large-bodied, and/or feed at high trophic levels are more likely to become locally extinct in habitat fragments (Woodroffe & Ginsberg 1998; Laurance *et al*. 2002). This has led to calls for conservation action at the sea- or landscape scale to mitigate threats to such species beyond protected areas (Soulé & Terborgh 1999; Lens *et al*. 2002; Sanderson *et al*. 2002). Further studies suggest that conservation at broad scales is also essential to maintain the seasonal migrations of many bird, mammal, and turtle species (Janzen 1986), as recognized by the Convention on Migratory Species. This has stimulated a robust debate over the conservation value of biological corridors (Beier & Noss 1998). More recently, the case for taking a sea- or landscape approach has been bolstered by consideration of broad-scale ecological processes, such as freshwater processes and disturbance regimes, that are critical to the persistence of species within sites (Balmford *et al*. 1998; Pressey *et al*. 2003). Conversely, many globally threatened species are now confined to single sites (Ricketts *et al*. 2005), and protected areas may provide the only immediate conservation option for some area-demanding species subject to intensive exploitation pressures (Emslie & Brooks 1999).

Advancing this debate requires a systematic assessment of threatened species that urgently require conservation action at the sea- or landscape scale. Here, we bring the new, comprehensive species assessments of the IUCN Red List of Threatened Species (Rodrigues *et al*. 2006) to bear on this question. The 2006 IUCN Red List (IUCN 2006) covers most tetrapods, including 4,856 mammals, 9,934 birds, 205 tortoises and turtles, and 5,918 amphibians. We limit consideration to these four taxa (hereafter collectively termed "tetrapods") that have been comprehensively assessed to minimize geographic bias. Using consistent categorization criteria, we review data for the 4,239 globally threatened species (i.e., *Critically Endangered* [CR], *Endangered* [EN], or *Vulnerable* [VU]) within these four taxa to determine the most appropriate spatial scale of conservation action for each species in the short- to medium term (i.e., mostly 10 years, but up to 100 depending on species—the same time frame as that over which the IUCN Red List measures extinction risk).

Methods

We categorized the spatial-scale requirements for *in situ* conservation of globally threatened species into four categories (Figure 1). At one extreme are those species for which effectively the entire global population is restricted to, and able to be conserved at, a single site (Figure 1A), where a "site" is a homogenous area that can be delineated and actually or potentially managed for conservation as a single unit (Fishpool & Evans 2001; Eken *et al*. 2004; Ricketts *et al*. 2005). Although site size tends to scale with the proportion of habitat remaining in a region, 82% of management units identified for globally threatened birds ($n = 4{,}493$) are smaller than 1,000 km^2 (BirdLife International 2006). An example is the frog, *Eleutherodactylus corona* (CR), which is restricted to 10 km^2 in the Massif de la Hotte in Haiti (Hedges & Thomas 1992). For species that currently only occur at a single site, the most urgent conservation action is to protect that

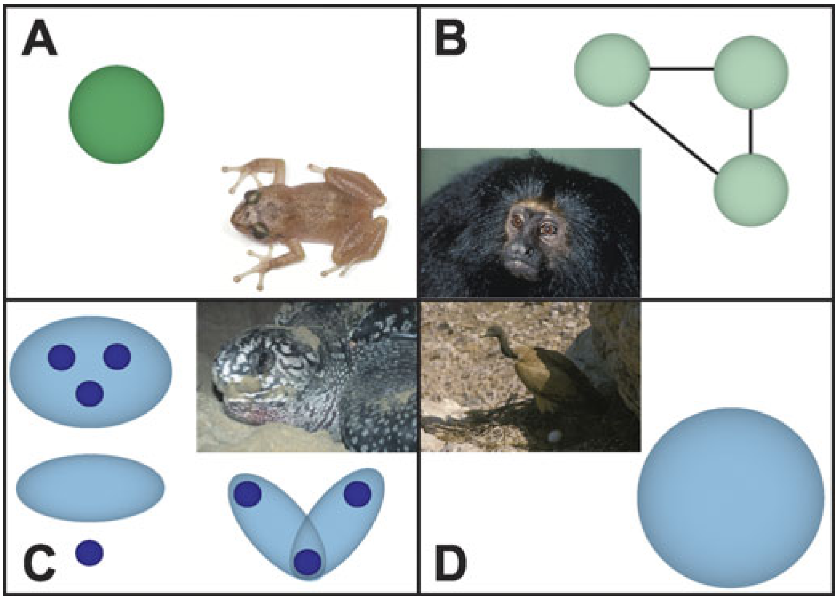

Figure 1 Scale requirements for the conservation of globally threatened species in the short- to medium term. A = dark green, species best conserved at a single site (e.g., *Eleutherodactylus corona*); B = pale green, species best conserved at a network of sites (e.g., black lion tamarin, *Leontopithecus chrysopygus*); C = dark blue, species best conserved at a network of sites complemented by broad-scale conservation action (e.g., leatherback turtle, *Dermochelys coriacea*); D = pale blue, species best conserved through broad-scale conservation action (e.g. Indian vulture, *Gyps indicus*). Photographs by S. B. Hedges (A), R. A. Mittermeier (B), O. Langrand (C), and A. Rahmani (D).

site. If the species is not naturally endemic to the site, but has been restricted to the site by anthropogenic pressures, then a longer-term conservation strategy may well involve expanding the number of sites occupied. This category does not include species that are only seasonally dependent on single sites, such as the whooping crane, *Grus americana* (EN) (Meine & Archibald 1996), and those that are threatened by changes in broad-scale ecological processes, such as the frog, *Telmatobius atacamensis* (CR), from the Argentinian Monte, which faces water pollution and catchment degradation originating far beyond its single site (Lavilla 2002).

The second category of species comprises those that occur only within multiple discrete sites (Figure 1B). This includes species threatened by forces originating beyond the boundaries of these sites, such as wildlife trade, but which can be effectively conserved in the short- to medium term by actions taken to safeguard the species within the network of sites. An example is the black lion tamarin, *Leontopithecus chrysopygus* (CR), from the Brazilian Atlantic forest, which now occurs in nine isolated forest fragments with a total area of 438 km^2 and is threatened primarily by habitat loss at these sites (Valladares-Padua *et al*. 2002). In the case of migratory species and those that now occur in small, isolated subpopulations due to habitat fragmentation, the sites where they survive need to be managed as a coordinated network. In the longer term, site-scale actions will likely need to be supported by broad-scale approaches, such as the restoration of connectivity.

Species for which sites are essential but insufficient even in the short- to medium term comprise the third category (Figure 1C). These species are best conserved through a combination of site-scale and broad-scale action, where "broad scale" refers to sea- or landscape scale and is defined by the needs of the species in question (Sanderson *et al*. 2002). An example is the leatherback turtle, *Dermochelys coriacea* (CR), which nests at discrete beaches where it is threatened by egg collection, but otherwise occurs throughout the tropical and temperate oceans where it is threatened by accidental bycatch and pollution (Chan & Liew 1996). Many such species are "area-demanding" in that they either regularly move between sites or naturally occur at such low densities during part or all of their life cycles such that it is not feasible to safeguard sites of adequate size. Others are threatened by changes in broad-scale ecological processes, such as freshwater flow regimes and water quality, fire and other disturbance regimes, and trophic interactions involving area-demanding species (e.g., reduced populations of the ungulate prey base for large carnivores such as the dhole *Cuon alpinus* (EN) (Sillero-Zubiri *et al*. 2004). For some species in this category, alternative strategies may lie at different ends of the spectrum with trade-offs between site-scale and broad-scale conservation action, but a combination of both is generally required.

The fourth category comprises species that are highly nomadic or consistently occur at low densities, such that sites alone are unable to support viable populations, and face threats that cannot be addressed at the site scale (Figure 1D). These species are best conserved through broad-scale action only. Species in this category include the Indian vulture *Gyps indicus* (CR), threatened by poisoning from feeding on dead livestock that have been treated with the veterinary drug diclofenac (Oaks *et al*. 2004). In most cases, conservation action on the ground will need to be complemented by action at the policy level (e.g., addressing population growth, economic alternatives, political priorities, and environmental awareness).

Results

In terms of *in situ* conservation, nearly one-fifth of threatened species (793 species; 20%) can be conserved at single sites, and approximately two-thirds (2500 species; 62%) through networks of sites in the short- to medium term. Most remaining threatened species (749 species; 18%) require site-scale conservation complemented by conservation action at the sea- or landscape scale, with less than 1% of threatened species (15 species) requiring conservation action at broad scales alone. Insufficient information is available to determine the required scale of conservation action for 182 species (4% of threatened species), which we therefore exclude from our statistics throughout. Furthermore, for some CR species, such as the 317 amphibians (17%) threatened by the disease chytridiomycosis (Baillie *et al*. 2004), *in situ* conservation needs to be complemented by captive breeding; and in most cases, broad-scale conservation action on the ground needs to be complemented by policy action at a range of levels. For example, reducing hunting pressure on area-demanding threatened species demands a combination of appropriate legislation and effective enforcement.

Discussion

Analysis of the distribution of threatened species among these categories by biome and taxon provides valuable insights for conservation planning (Figure 2). The distribution varies by biome ($G = 667.68$, df = 6, $P < 0.0001$). For threatened marine tetrapods, the need for broad-scale conservation action is overwhelming, with 74% of species urgently requiring conservation action at

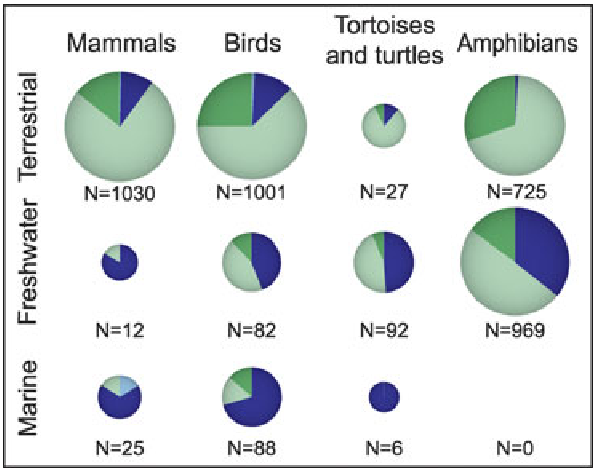

Figure 2 Percentages of globally threatened species requiring different scales of conservation action in the short- to medium term. Dark green = species best conserved at a single site; pale green = species best conserved at a network of sites; dark blue = species best conserved at a network of sites complemented by broad-scale conservation action; pale blue = species best conserved through broad-scale conservation action. The totals exclude species insufficiently known to assess the appropriate scale required. Relative size of pies corresponds to the number of species in each taxon/biome combination.

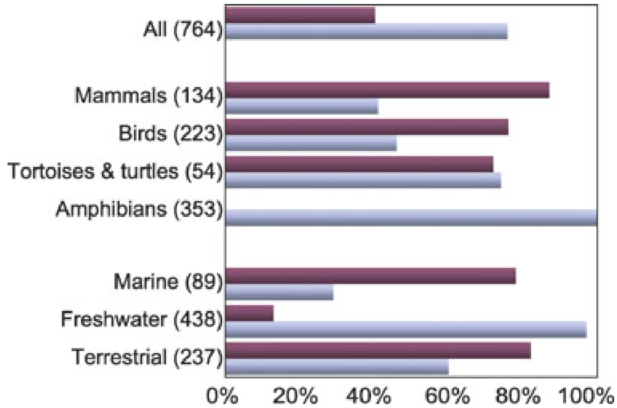

Figure 3 Percentages of globally threatened species requiring broad-scale conservation action in the short- to medium term that are (a) area-demanding (maroon) and/or (b) dependent on broad-scale ecological processes (mauve). The two categories are not mutually exclusive.

the seascape scale (either in combination with sites or alone). The equivalent figure is also high for threatened freshwater species (38%), but much lower for threatened terrestrial species (8%). This result comes with the caveat that marine species are currently poorly represented on the IUCN Red List, and so our study was limited to the inclusion of 119 threatened species. The trend for marine species to possess broad-scale conservation requirements probably reflects greater site permeability and species mobility in marine systems (Carr *et al.* 2003). We also find differences among mammals, birds, tortoises and turtles, and amphibians ($G = 160.15$, df = 9, $P < 0.0001$). Of globally threatened mammals, 13% require conservation action at the sea- or landscape scale in the short- to medium term (usually in combination with sites). This figure is higher for birds and amphibians, at 19% and 21%, respectively, and much higher (43%) for tortoises and turtles. Figure 2 reveals greater similarities within each biome across taxa than within each taxon across biomes. However, hierarchical log-linear analysis (excluding marine species) indicates that the three-dimensional model provides the best fit (i.e., category is dependent on both biome and taxon) (likelihood ratio $\chi^2 = 41.20$, df = 9, $P < 0.0001$).

The case for broad-scale conservation action has generally focused on area-demanding species (Woodroffe & Ginsberg 1998; Terborgh *et al.* 1999; Sanderson *et al.* 2002). However, of the 764 globally threatened tetrapods requiring sea- or landscape-scale conservation, just 43% are area-demanding compared to 72% threatened by changes in broad-scale ecological processes (15% require broad-scale conservation due to both factors) (Figure 3). These ecological processes include water quality (impacting 53% of species requiring broad-scale action), freshwater flow regimes (25%), trophic interactions involving area-demanding species (10%), and grazing and land-use intensification (7%). By contrast, direct threats to area-demanding species comprise primarily exploitation and persecution (26%) and incidental mortality (12%). Other issues such as modification of fire regimes, disease, and invasive species that cannot be addressed at the site scale alone are currently minor (3%). The IUCN Red List identifies relatively few species as threatened specifically by climate change at present (Baillie *et al.* 2004), because likely responses of most species are not yet understood well enough to estimate extinction risks or determine the spatial scale of effective conservation responses (Akçakaya *et al.* 2006).

The geographical distribution of threatened tetrapods requiring urgent conservation action at the sea- or landscape scale (Figure 4A) reflects the distribution of threatened species overall (Baillie *et al.* 2004). However, the different issues driving the need for broad-scale conservation action have distinctive spatial signatures. The highest densities of terrestrial and freshwater species requiring broad-scale conservation action to address exploitation and persecution occur in Asia and northern South America, whereas marine species facing similar threats are concentrated in the northern oceans (Figure 4B). The Ganges and Amazon Rivers together with the southern oceans harbor most species needing urgent broad-scale conservation action to address incidental mortality (Figure 4C).

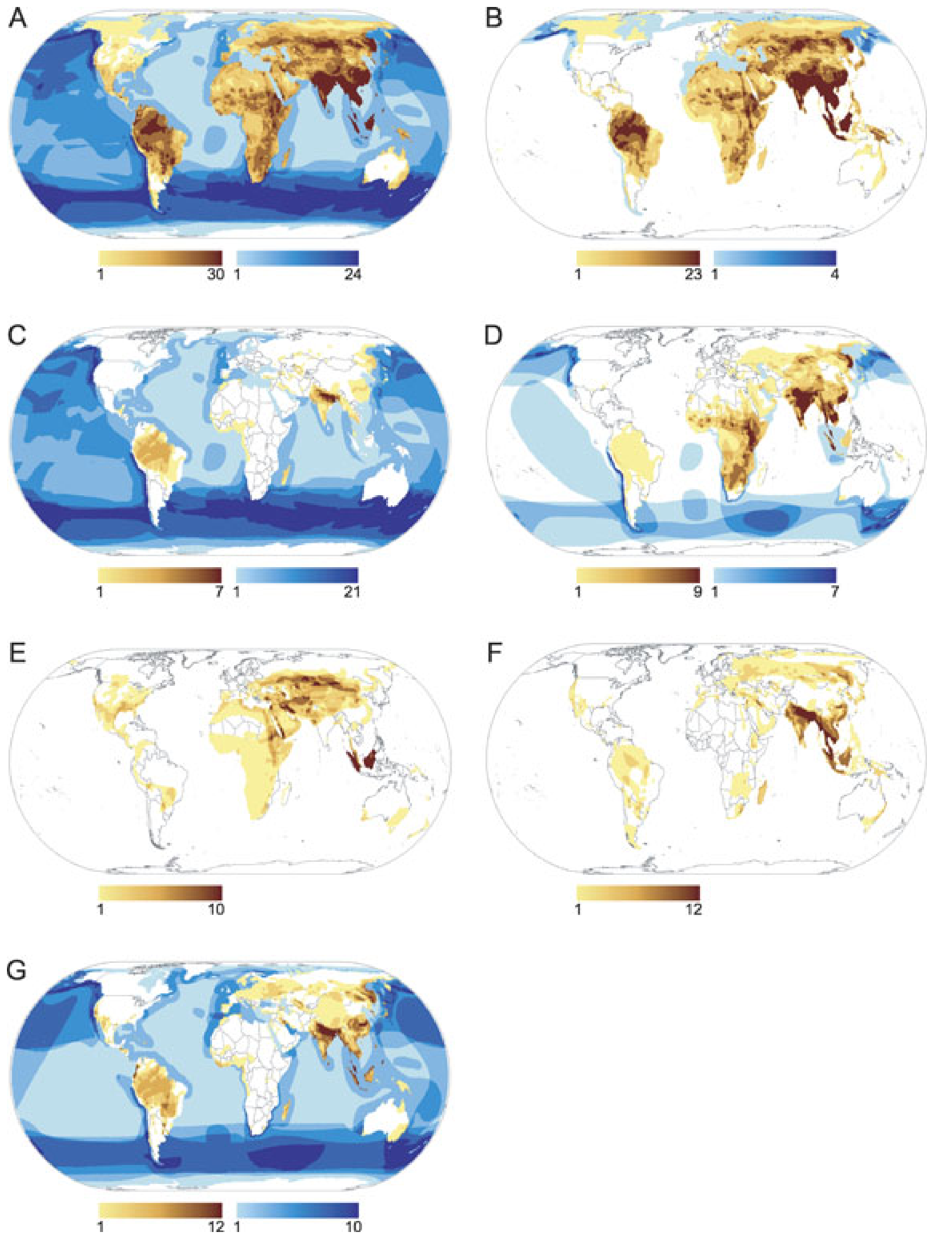

Figure 4 Richness map of globally threatened species requiring urgent conservation action at a sea- or landscape-scale in the short- to medium term to address: (A) all threats, (B) exploitation and persecution, (C) incidental mortality, (D) trophic interactions, (E) grazing and land-use intensification, (F) water flows, and (G) water quality. Color scale based on five equal-area classes.

Species requiring broad-scale action to address trophic interactions occur mainly in Asia and southern and eastern Africa on land, and in both the southern and northern oceans (Figure 4D). The highest densities of species requiring conservation action at a landscape scale to address grazing and land-use intensification occur in central Asia and Indonesia (Figure 4E), whereas alteration of freshwater flow regimes highlights southern Asia (Figure 4F). Species requiring broad-scale action to address freshwater quality issues are concentrated in Asia and the Andes, and although sea water quality is an issue across the oceans as a whole, its impacts are again concentrated in the northern and southern oceans, especially in areas close to inhabited land masses (Figure 4G). Spatial plans and systematic conservation planning exercises must look beyond sites to include the additional area and connectivity requirements of these threatened species. Conservation action in these spaces does not necessarily require preservation of intact habitat, but may include more effective enforcement to reduce illegal exploitation of threatened species, changes in fishing gear to reduce incidental mortality, and adjustments to livestock management to reduce conflicts over fencing and grazing and water resources.

Conclusions

These results demonstrate that site protection should remain the cornerstone of conservation strategies for most globally threatened tetrapods (over 99%). However, conservation action beyond these sites is also required for at least one-fifth of threatened species. We restricted our analysis to the same short- to medium-term time frame used by the IUCN Red List in measuring extinction risk. Over longer time frames, a larger proportion of threatened species will require conservation action at a sea- or landscape scale, for example, in response to slower-acting threats such as habitat fragmentation (Brooks *et al.* 1999). In addition, some area-demanding species, such as large carnivores, play important functional roles necessary for the persistence of threatened species and ecosystems (Terborgh *et al.* 1999), and thus merit conservation action at the sea- or landscape scale to address localized declines even though they are not themselves globally threatened. Finally, it is also essential to address the underlying causes of threats to biodiversity at local, national, and international policy levels. This includes coordinated strategic action to address global threats to entire assemblages of species, such as disease in amphibians (Mendelson *et al.* 2006) and climate change (Thomas *et al.* 2004). Nonetheless, our key conclusion is that neither site-scale nor broad-scale approaches alone can prevent mass extinction. Rather, although site protection must remain the cornerstone for threatened species conservation, urgent intervention at the sea- or landscape scale is also essential for effective biodiversity conservation.

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1. Supporting information on methods.

Table S1a. Globally threatened mammals.

Table S1b. Globally threatened birds.

Table S1c. Globally threatened turtles and tortoises.

Table S1d. Globally threatened amphibians.

Table S2a. Globally threatened mammals that require broad-scale conservation action.

Table S2b. Globally threatened birds that require broad-scale conservation action.

Table S2c. Globally threatened turtles and tortoises that require broad-scale conservation action.

Table S2d. Globally threatened amphibians that require broad-scale conservation action.

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