Mammal Population Losses and the Extinction Crisis

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The disappearance of populations is a prelude to species extinction. No graphically explicit estimates have been made of current population losses of major indicator taxa. Here we compare historic and present distributions of 173 declining mammal species from six continents. These species have collectively lost over 50% of their historic range area, mostly where human activities are intensive. This implies a serious loss of ecosystem services and goods. It also signals a substantial threat to species diversity.

Population extinctions are a more sensitive indicator of the loss of biological capital than species extinctions. This is because many of the species that have lost a substantial portion of their populations [thus altering ecosystems and perhaps reducing the ability of those systems to deliver services (I)] are unlikely to go globally extinct and enter the species extinction statistics in the foreseeable future (2). Most analyses of the current loss of biodiversity emphasize species extinctions (3–5) and patterns of species decline (6–8) and do not convey the true extent of the depletion of humanity’s natural capital. To measure that depletion, we need to analyze extinctions of both populations and species. Here we give a rough minimum estimate of the global loss of continental mammal populations. We believe that mammals, because of their great taxonomic diversity and the wide range of ecological niches they exploit, can serve as an indicator of what is occurring in the rest of Earth’s biota.

Our data consist of historic (i.e., mostly 19th century) and present-day distributional ranges of all of the terrestrial mammals of Australia and subsets of the terrestrial mammal faunas of Africa, South East Asia, Europe, and North and South America (Table 1 and table S1). These subsets consist of all mammal species whose ranges are known to be shrinking for which we had access to data. They comprise roughly 4% of the ~4650 known species. We assume that loss of range area is due to the extinction of populations, but we do not attempt to equate a given areal loss with a precise number of population extinctions due to the complexities of defining and delimiting populations (9). Data were gathered from the specialized literature (Web references). In general, because they are better known, most of our range data are from medium- and large-sized species. Whether globally these are more or less liable to population extinction than medium to small species is a matter of conjecture (10–12), but at present there is little reason to assume an important directional bias in our samples. There was no correlation between body mass and range shrinkage in our data (P > 0.05, r2 = 0.22). There does remain a possible source of bias in the relative lack of very small species in the total sample (12).

The ranges were digitized and the historic and present range areas were calculated. For each species, we estimated both total area occupied historically and percent historic range area now occupied. Using ArcView 3.1, the ranges were superimposed to produce synthetic maps summarizing the losses of species populations in 2 degree by 2 degree quadrats [i.e., the number of species that have disappeared from each quadrant because all of their populations previously located in that quadrant have disappeared]. The area of these quadrats, of course, varies with latitude, but the average of such quadrats over land is about 30,000 km².

Declining species of mammals in our sample had lost from 3 to 100% of their
geographic ranges (mean 68 ± SE 2.46), but range lost was above 50% for most (72%) species (Table 1). Species such as Pere David’s deer (Elaphurus davidianus), which is extinct in the wild, lost 100%, whereas others like Spotted hyena (Crocuta crocuta) that have a higher tolerance for human disturbance lost 14%. As expected, there were striking differences between the continents, as shown in Table 1 and Figure 1. The number of populations lost has been greater in areas that are both large and species rich (e.g., Africa and Southeast Asia).

In our analysis, population extinctions today seem to be concentrated either where there are high human population densities, or where other human impacts, such as intensive agriculture, grazing, and hunting, have been severe. Larger mammals are often hunted to extinction or have their habitats preempted (13, 14). The mammal faunal sample from Southeast Asia shows one of the highest losses of species ranges and, thus, of mammal population extinctions: 57% of its quadrats have lost between 75 and 100% of their mammals. In Southeast Asia, human population density is extremely high (e.g., Indonesia, 115 persons/km²; China, 130 persons/km²; Pakistan, 190 persons/km²; India, 305 persons/km²). Similarly, in North America, the highest percentage losses are in the heavily populated eastern United States.

In Africa, the areas with the highest levels of mammal population extinction do not coincide as well with high human population densities (e.g., Nigeria has 135 persons/km²), even though there is a positive correlation of human population density with species richness in general (15). Rather, the highest percentage of population extinctions have occurred in the region of the Sahara (Mali, 4 persons/km²; Mauritania, 1.5 persons/km²), presumably because gazelles and other large herbivores have been hunted to extinction by local people and sport hunters and because of anthropogenic desertification and competition with domestic animals for scarce forage and water (16). In recent years, many populations of tropical species such as gorillas (Gorilla gorilla) and drills (Mandrillus leucophaeus) have been lost in equatorial Africa (e.g., Congo, where there are 20 persons/km²) (17, 18), but there are no good data on their present geographic ranges. In southern Africa, not surprisingly, the absolute number of extinctions coincides with high population densities of Homo sapiens.

Understandably, Australia, which is the continent with the largest number of mammal species extinctions (12, 19), is also a continent showing a widespread severe reduction of populations. Factors causing population and species extinctions there are mainly related to overgrazing, agriculture, forestry practices (including altered fire regimes) (20), and, especially, the large numbers of introduced predators and competitors (21–24).

In South America, population losses are heaviest in the intensively agricultural southern plains (Pampas region in Argentina),...
prominent species, underrepresented in our sample, have lost portions of their ranges but without detection because they have not been subject to intensive mapping attempts.

The second probable conservative bias is potentially even greater. Distribution maps of historic ranges necessarily neglect the many smaller gaps in the distribution representing areas of unsuitable habitat (to take an obvious case, lakes and rivers do not ordinarily appear as blanks in the middle of prairie dog distributions). But we can be sure that anthropogenic habitat alteration has generally created much bigger gaps in the continuous maps that represent present distributions. For example, the map in the standard butterfly guide (29) shows the intensely studied Euphydryas editha as still occupying almost all of California except the Central Valley. In reality, population extinctions in historic times have removed it from many, if not most, of the sites where it occurred previously (30). Similarly, several species such as the monkeys Leontopithecus rosalia and Brachyteles arachnoides in the Mata Atlantica or the marsupials Phascogale calura and Smynthopsis longicaudata in Australia have had their historic ranges reduced to tiny fragments of habitat (12, 19, 25). Nonetheless, they are shown in our present maps as occupying entire quadrats, even though the vast majority of the populations in those quadrats have already gone extinct. If such smaller scale but nearly ubiquitous differences between historic and present mammal distributions could be calculated, losses of area and populations would be much greater.

There is a need to determine more precisely the proportion of mammal species that are shrinking on continents other than Australia, the one continent that has been relatively thoroughly studied, and to investigate the relation of vulnerability to population extinction with respect to body size and other variables on those continents. Also, studies of the details of “range filling” in mammals and other organisms will be critical to measuring more accurately the magnitude of population extinctions. An especially difficult problem is to translate between loss of range area and extinction of populations (9).

By definition, conserving population diversity means spreading conservation efforts over wider regions as a complement to important efforts to preserve “hotspots” of species richness (31, 32). Such a regional approach will be made more difficult by the problems of what we call “political endemism,” the limitation through population extinction of a species’ geographic range to one or a few political entities. In some cases, if such political entities are not as interested (or capable) in conservation as other entities in the historic range, that may ensure eventual extinction (33). A combination of political endemism and political instability has certainly made the fates of the black (Diceros bicornis) and Sumatran (Diceros sumatrensis) rhinos much more uncertain (34). In both of these conservation cases, a high priority would be to reestablish populations not only over a broader geographic range, but also within a greater variety of countries.

The loss of species diversity has correctly attracted much attention from the general public and decision-makers. It is now the job of the community of environmental scientists to give equal prominence to the issue of the loss of population diversity.

References and Notes

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Table 1. Average area losses in mammals whose ranges have contracted. Samples were taken from six continents. Asterisk indicates value is from raw data, not from columns to the left.

<table>
<thead>
<tr>
<th>Continent</th>
<th>No. of species</th>
<th>Historic range (km²/1000)</th>
<th>Present range (km²/1000)</th>
<th>Range lost (km²/1000)</th>
<th>% Range lost*</th>
</tr>
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<td>52</td>
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<td>2046</td>
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<td>819</td>
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<td>2293</td>
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<td></td>
<td>3599</td>
<td>1569</td>
<td>2030</td>
<td>68</td>
</tr>
</tbody>
</table>
R E P O R T S

beater’s Passum using Population Viability Analysis (Centre for Resource and Environmental Studies, Australian National University, Canberra, 1995).


35. We thank I. Salazar, G. Oliva, and J. Pacheco for helping gather the data and with the spatial analyses. We are indebted to J. Brown and G. Daily for extensive discussions of the ideas presented here and for reviewing the manuscript. J. Diamond, G. Luck, M. Mayfield, H. Mooney, S. Pittman, J. Rehman, and C. Sekercioglu also kindly criticized drafts of this paper. The comments by M. Lomolino and an anonymous reviewer improved the manuscript. Funded by the Universidad Nacional Autónoma de México, the Koret Foundation, the Joyce Mertz-Gilmore Foundation, and the Wenslow Foundation.

Supporting Online Material (www.sciencemag.org/cgi/content/full/296/5569/904/DC1) Table S1 References and notes

26 December 2001; accepted 20 March 2002

Genomewide Analysis of mRNA Processing in Yeast Using Splicing-Specific Microarrays
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Introns interrupt almost every eukaryotic protein-coding gene, yet how the splicing apparatus interprets the genome during messenger RNA (mRNA) synthesis is poorly understood. We designed microarrays to distinguish spliced from unspliced RNA for each intron-containing yeast gene and measured genomewide effects on splicing caused by loss of 18 different mRNA processing factors. After accommodating changes in transcription and decay by using gene-specific indexes, functional relationships between mRNA processing factors can be identified through their common effects on spliced and unspliced RNA. Groups of genes with different dependencies on mRNA processing factors are also apparent. Quantitative polymerase chain reactions confirm the array-based finding that Prp17p and Prp18p are not dispensable for removal of introns with short branchpoint-to-3′ splice site distances.

Protein-coding information in eukaryotic genomes is fragmented into exons, which must be recognized and joined by the process of RNA splicing. Splicing takes place in the nucleus within a dynamic ribonucleoprotein complex called the spliceosome (1). The spliceosome transforms information within transcripts of the eukaryotic genome to create sequences not found in DNA. By its nature and position in the gene expression pathway, splicing expands the possible interpretations of genomic information and does so under developmental and environmental influence (2). Our understanding of the process of splicing is derived from studies on relatively few introns. As eukaryotic genomes are sequenced, it has become necessary to ask how the process of splicing is integrated into genome function and evolution. Compared with higher eukaryotes, yeast contains relatively few spliceosomal introns, and most have been correctly annotated (3, 4). Hence, we chose to perform genomewide study of splicing in the yeast Saccharomyces cerevisiae.

To discriminate between spliced and unspliced RNAs for each intron-containing yeast gene, we used DNA microarrays (3, 5). Oligonucleotides were designed to detect the splice junction (specific to spliced RNA and not found in the genome), the intron (present in unspliced RNA), and the second exon (common to spliced and unspliced RNA) for each intron-containing gene as shown in Figure 1A. The oligonucleotides were printed on glass slides to create splicing-sensitive microarrays for yeast (7).

To determine whether oligonucleotide arrays can function as genomewide sensors of splicing, we compared RNA of cells carrying the temperature-sensitive splicing mutation prp4-1, which causes widespread intron accumulation and loss of splice junction sequences relative to wild type (Fig. 1C, left). The effect of each deletion on spliced and unspliced RNA is different. Most severe is prp18Δ, which causes widespread intron accumulation and loss of splice junction sequences relative to wild type (Fig. 1C, left). The cys2Δ mutation enhances defects in U2 small nuclear RNA (snRNA) or Prp5p (11, 12) but causes little intron accumulation (Fig. 1C, center). Although not required for splicing, Dbr1p debranches the lariat, and its loss results in the dramatic accumulation of intron lariats (13). In the dbr1Δ strain, most introns accumulate, and there is little effect on spliced mRNAs (Fig. 1C, right). This demonstrates that qualitative differences in splicing phenotype can be distinguished by using splicing sensitive microarrays.

Changes in spliced and unspliced RNA levels due to loss of an mRNA processing factor may arise directly from splicing inhibition or may be due to secondary events that alter transcription or RNA decay. For example, signal from a splice junction probe may increase for a gene whose transcription is induced, even though splicing is inhibited. To

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34. We thank I. Salazar, G. Oliva, and J. Pacheco for helping gather the data and with the spatial analyses. We are indebted to J. Brown and G. Daily for extensive discussions of the ideas presented here and for reviewing the manuscript. J. Diamond, G. Luck, M. Mayfield, H. Mooney, S. Pittman, J. Rehman, and C. Sekercioglu also kindly criticized drafts of this paper. The comments by M. Lomolino and an anonymous reviewer improved the manuscript. Funded by the Universidad Nacional Autónoma de México, the Koret Foundation, the Joyce Mertz-Gilmore Foundation, and the Wenslow Foundation.

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