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Seven forms of rarity in mammals

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Abstract

Conservation biologists have identified threats to the survival of about a quarter of the mammalian species; to identify patterns of rarity and commonness of mammals, we studied a global sample of 1212 species (about 28% of the mammals) using the '7 forms of rarity' model (in which species are roughly divided into above and below the median for local population density, species' range area, and number of habitat types).

From a niche-based hypothesis of abundance and distribution, we predicted that mammals would exhibit a bimodal pattern of rarity and commonness, with an overabundance of species in the relatively rarest and most common categories; and just such a significant bimodal pattern emerged, with over a quarter of the species classified as exceedingly rare and a further quarter very common, supporting the niche-based hypothesis.

Orders that include large mammals, including perissodactyls, primates, diprotodonts, and carnivores, exhibited significantly high proportions of relatively rare species; and tropical zoogeographic regions, especially Indomalaya, had relatively high proportions of species in the rarest category.

Significant biases in the available data on mammals included under-sampling of small species like rodents and bats, and a relative paucity of data on zoogeographic regions outside of North America and Australia.

Mammalian species listed as of conservation concern by the IUCN occurred in all cells of the model, indicating that even relatively common species can be listed as threatened under some conditions; but we also found that sixty-three species were relatively rare in all three criteria of the 7-forms model but were not listed as threatened, indicating potential candidates for further study.

Mammals may be a group of animals where rarity or commonness is a natural aspect of species biology, both confirming and perhaps partly explaining the large proportion of mammals assigned threatened status.

Keywords

Conservation biology, IUCN, Mammalia, niche based hypothesis, rare species, 7 forms of rarity, zoogeography.

INTRODUCTION

As a group of organisms, mammals have attracted strong concern from conservation biologists, with about one-fourth of the species listed as endangered or threatened in some way (IUCN, 1997). The World Conservation Union (IUCN) attempts to promote an adaptive management approach to protecting mammalian species by summarizing currently available information and categorizing species according to their likelihood of extinction (IUCN, 1994). As more information on mammalian species becomes available, these efforts should improve, resulting in limited conservation resources being placed where they can provide the greatest benefit. Through the IUCN's listing of such a high proportion of the mammalian species, attention and resources will necessarily focus on this group of organisms.

In order to improve conservation efforts, it is necessary to understand natural processes that result in threats to species. Thus, such theoretical fields as population ecology and evolutionary biology need to keep pace with attempts at informed management of threatened species (Ehrlich & Wilson, 1991; Wilson, 1992; Gaston, 1994; Ceballos & Brown, 1995). Basic research can produce improved decisions about which species are most threatened, and lead to fresh evaluations of potential and actual conservation actions. For example, the fact that fully one-fourth of the mammalian species are considered threatened by the IUCN is a stunning and sobering result. To put this result in context, however, we

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need to understand why mammals are so prone to threats to their existence, and whether in fact such a pattern prevails. For these questions, we need to know whether mammalian species have a natural tendency to become rare, and to evaluate what kinds of rarity typically occur among mammalian species.

The IUCN's criteria for listing species as threatened depend fairly strongly on temporal changes in the numbers of individuals in populations or species (IUCN, 1994; Dobson *et al*., 1997). In many cases, however, information on even the well-known mammalian species is lacking or incomplete, so that species are listed as 'data deficient.' Thus, information about population trends for even the relatively well-known mammalian species ranges from scanty to fairly complete (Dobson *et al*., 1997), forcing the confidence of classification for threatened species to vary. Determination of the rarity of species requires less information than the classification of threat or endangerment, but it has the disadvantage of including species that exhibit natural rarity, perhaps without major threat of extinction (Dobson *et al*., 1995; Gaston & Blackburn, 1995). Studies of rarity have some advantages, however, such as identification of species that require further conservation study (Caughley, 1994; Dobson *et al*., 1995; Dobson *et al*., 1997), and comparison of rare and common species (Thomas & Mallorie, 1985; Arita *et al*., 1990; Kattan, 1992; McCoy & Mushinsky, 1992; Dobson & Yu, 1993).

Unlike species-specific studies of extinction threat, studies of rarity and commonness facilitate macroecological comparisons that may lead to tests of hypotheses about underlying processes (e.g. Brown, 1995). To facilitate and improve conservation practice, it is important to understand possible causes of the high proportion of rare species among the mammals. While human activities might be expected to impact such large animals as mammals, we also need to know whether this group of species has a natural tendency to have a large proportion of relatively rare species. Brown (1984) noted that such taxa as mammals often exhibit a bimodal pattern of many species being extremely common and extremely rare, and suggested a 'niche-based' hypothesis that this pattern reflects a natural tendency for species to be either habitat generalists or specialists.

The purpose of our study was to examine rarity and commonness of a large sample of species from the mammalian fauna of the world. Our concept of rarity was based on Rabinowitz's '7 forms of rarity' model, that incorporates information about local population density, geographical range, and variety of habitats occupied by a species (Rabinowitz, 1981; Rabinowitz *et al*., 1986). An advantage of the 7 forms of rarity model is that it requires minimal information, but the requirement of quantitative data for all three of the variables mentioned above caused exclusion of some potential sources of information. Within the confines of this stricture, however, we attempted to find as many species as possible for inclusion.

We had several specific objectives in this study. First, we wanted to examine whether the classification of one-fourth of the mammalian species as threatened seemed justified, using a somewhat independent 'static' approach to the classification of potential threat to species (Dobson *et al*., 1997). Even though evaluation of rarity does not necessarily indicate threat of extinction, species generally become rare before they go extinct (Dobson *et al*., 1995). Second, we hoped to identify the types of rarity that are most common in mammals. Third, examination of the types of rarity might indicate processes that predispose mammals to be threatened, and we specifically asked whether the available data were consistent with Brown's (1984) niche-based hypothesis. Finally, and most importantly, we hoped to identify biogeographical patterns of distribution of rare species, especially numbers and proportions of species that have sufficient information on mammalian rarity and commonness in different zoogeographic regions.

MATERIALS AND METHODS

Rabinowitz's (1981; Rabinowitz *et al*., 1986) 7 forms of rarity model focuses on three characteristics of species that are often available in the literature: (1) local population density (2) the area of the species range, and (3) the number of different kinds of habitats that species occupy. If species are dichotomized for each of these variables, an eight-celled model is created that reflects different types of rarity and commonness (Fig. 1, modified from Rabinowitz, 1981). Species above and below the median for all three characteristics can be thought of as being relatively common and relatively rare, respectively, in comparison with other species. Species in other categories have intermediate degrees of rarity because they exhibit relative rarity (or commonness) in only one or two of the characteristics. We assigned a rank rarity score to each of the eight cells of the model by adding 1 to the number of the three characteristics of species that exhibited values above the median (Fig. 1).

Body size is another characteristic of species that can have a strong influence on the cell into which species are placed, due to significant associations of body size with population density and species' range area (Arita *et al*., 1990; Dobson & Yu, 1993; Dobson *et al*., 1995). Thus, we incorporated body mass into our analyses, but in the interest of including as many species as possible, our procedures were necessarily qualitative. Our dichotomizations used arbitrary criteria to divide species exhibiting each characteristic (viz., local density, area of species range, and number of habitats) into two

		DISTRIBUTION			
		large		small	
POPULATION		high	low	high	low
HABITAT	broad	A (4)	C (3)	E (3)	G (2)
	narrow	B (3)	D (2)	F (2)	H (1)

Figure 1 Classes of rarity after Rabinowitz (1981) and ranks of rarity that were assigned to each cell. Category H contains species rare in all three factors, and a rank of 1 indicates the highest degree of rarity.

approximately equal groups. Small mammals (mean body mass less than 100 g) with densities of 100/km^2 or higher were considered to be above the median, and lower densities were below the median. In medium-sized mammals (body mass between 100 g and 30 kg), densities greater than 1/km^2 were designated as above the median. In large mammals (above 30 kg), densities greater than 1/100 km^2 were above the median. Our arbitrary body size classifications divided the species into three roughly equal groupings, and were not meant to define such terms as 'small mammals', that often include other ranges of body size.

Similar procedures were followed in dichotomizing distributional ranges of species. Ranges were above the median if they covered several provinces or a country (areas above 10,000 km^2), while ranges over a few counties or on a small island were considered to be below the median (areas of less than 10,000 km^2). For intermediate-sized ranges, we again incorporated influences of body size. Thus, intermediate ranges were considered to be above the median for smaller-sized species, and below the median for species that were above the median for body sizes. Of seven general habitat types, species were classified as above the median if they occupied two or more habitats, and below the median if they occupied only one habitat type. The general habitat types were forest, woodland, scrub, savanna, steppe, desert, and aquatic (Corbet & Hill, 1991). Zoogeographic regions were the Palearctic, Nearctic, Neotropical, Afrotropical, Indomalayan, and Australasian (Corbet & Hill, 1991).

Data were gathered from an extensive literature review. The most productive sources were IUCN Action Plans (those containing data on all species, common and rare, in a taxon), Mammalian Species Accounts (special publications of the American Society of Mammalogists, numbers 1 through 545), Grzimek's *Encyclopedia of mammals* (Parker, 1990), and the *Mammals of Australia* (Strathan, 1995). Of the roughly 4327 species of mammals (Corbet & Hill, 1991), we found sufficient information for inclusion of 1212 species (28.0% of the fauna). Designation of the Orders of mammals (as well as species names, see the Appendix) followed Wilson & Reeder (1993). Because the quality of the data necessarily varied, we identified species with relatively poor data (103 of 1212 species) and conducted all analyses with and without them. Results did not vary substantially between analyses, so we present only the results for all of the 1212 species.

The $2 \times 2 \times 2$ cells of the 7 forms of rarity model (Fig. 1) were examined with a three-way *G*-test (CATMOD procedure; SAS, 1990). Expected number of species in each cell were calculated assuming homogeneity (Bailey, 1959). Thus, the expected number of species in category A was: proportion of species above the median in density × proportion of species above the median in range area × proportion of species occurring in more than one habitat × the total number of species in the sample (expected number of species in other cells calculated similarly). Statistical significance was generally set at the $P = 0.05$ level. Other statistical analyses involved tests for homogeneity of groupings of species (χ^2-tests) and rank comparisons of rarity among mammalian Orders (Mann–Whitney *U*-tests, using scores from Fig. 1) (Sokal & Rohlf, 1981). Multiple post hoc pair-wise tests were also run, when the overall heterogeneity of the data set was significant. For post-hoc tests, some aspect of each grouping (e.g. % species in category H, mean rank of rarity for an Order, and percentage species from a biogeographic region in our sample) was compared to a sample consisting of all other groups. This procedure serves to indicate groupings that differ from other mammals qualitatively, but the comparisons were not statistically independent. Because several tests were run in these cases, statistical significance equivalent to the $\alpha = 0.05$ level was estimated as $\alpha' = 1 - (1 - \alpha)^{1/k}$, where k was the number of statistical comparisons (Sokal & Rohlf, 1981).

RESULTS

Samples of species varied considerably among Orders and categories of rarity, but about a quarter of the species fell into the most common category (cell A) and slightly more than another quarter fell into the most rare category (cell H, Table 1). This pattern was significant, with far more species extremely common and rare than would be expected by chance (Fig. 2; χ^2-test of homogeneity, $\chi^2 = 569.8$, d.f. = 7, $P < 0.0001$). Other cells in the 7 forms of rarity model had fewer species than expected; however, this pattern was not as extreme (compare the rest of the cells with A and H). A *G*-test indicated that characteristics of rarity interacted in pair-wise fashion: range area by population density ($\chi^2 = 141.0$, $P < 0.0001$), density by number of habitats occupied ($\chi^2 = 62.1$, $P < 0.0001$), and area by habitats ($\chi^2 = 66.2$, $P < 0.0001$). Once the pair–wise interactions were accounted for, no significant three–way interaction remained (area by density by habitats, $\chi^2 = 0.01$, $P = 0.93$).

We examined whether particular Orders contained high proportions of species in the rarest category, cell H (Table 2). Perissodactyls had the highest representation of rare species and bats had relatively low representation, but this pattern was not highly significant. When mean ranks of rarity for species in different Orders were examined, however, perissodactyls, primates, diprotodonts, and carnivores had significantly lower scores (more rare species) than expected (Table 3). In this analysis, bats exhibited significantly high scores. Sampled species were not distributed homogeneously among Orders, however, and rodents and bats in particular were under-sampled (Table 4). On the other extreme, our data set included all of the species of lagomorphs and tree shrews.

Zoogeographic regions that included tropical areas had the highest proportion of species in the rarest category, with over 40% of the species in the tropical Indomalayan region included (Table 5). The Nearctic region, on the other hand, had relatively few species in the rarest category. Sampling of zoogeographic regions was heterogeneous, however, with species highly significantly under-represented in the Neotropical and Afrotropical regions, and over-represented in the Nearctic and Australasian regions.

We compared the different forms of rarity that our analyses

Table 1 Number of species in each cell of the rarity model for mammals. Stars (* in parentheses) indicates numbers of included species with relatively poor data (see text).

Order	A	B	C	D	E	F	G	H	Total
Artiodactyla	14	5	4	4	2	4	4	$10^{(1*)}$	47
Carnivora	$33^{(1*)}$	$33^{(1*)}$	$15^{(1*)}$	$31^{(6*)}$	3	3	16	$62^{(1*)}$	196
Cetacea		8		4				3	15
Chiroptera	$61^{(9*)}$	$19^{(4*)}$	$21^{(4*)}$	$17^{(5*)}$	$2^{(1*)}$	7	$3^{(1*)}$	$28^{(9*)}$	158
Dasyuromorphia	9	5	2	3	7	7	6	13	52
Didelphimorpha	2		$2^{(1*)}$	$2^{(1*)}$				$2^{(1*)}$	8
Diprotodontia	15	5		1	6	19	2	25	73
Xenarthra	$2^{(1*)}$								2
Hyracoidea	1	$1^{(1*)}$							2
Insectivora	$74^{(2*)}$	$32^{(1*)}$	$5^{(2*)}$	$6^{(1*)}$	5	13	3	$70^{(4*)}$	208
Lagomorpha	20	9	1	5	7	$14^{(1*)}$	2	$20^{(3*)}$	78
Macroscelidea	1						1		2
Microbiotheria						$1^{(1*)}$			1
Monotremata	1				1				2
Notoryctemorpha		1							1
Paucituberculata								1	1
Peramelemorphia	4				2		1	1	8
Perissodactyla	1			1			1	9	12
Pholidota				3					3
Polyprotodontia	1								1
Primates	$4^{(1*)}$	$3^{(1*)}$	$4^{(2*)}$	$9^{(1*)}$	$6^{(1*)}$	$1^{(1*)}$	14	$19^{(2*)}$	60
Proboscidea			1					1	2
Rodentia	$71^{(9*)}$	$47^{(9*)}$	3	10	$20^{(1*)}$	$37^{(7*)}$	$7^{(2*)}$	$60^{(9*)}$	255
Scandentia	3	10				2		4	19
Sirenia				2				3	5
Tubulidentata				1					1
Total	317	178	58	99	61	108	60	331	1212

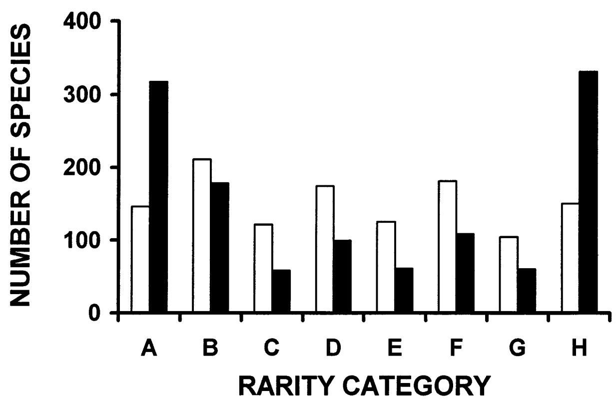

Figure 2 Number of species in each category of commonness or rarity (see Figure 1 for definitions of cells A through H). Open bars show the expected values calculated from the product of frequencies of species above or below the median for rarity/commonness variables (local population density, species' range, number of habitat types), multiplied times the total number of species in the sample. Solid bars show the actual number of species in each rarity category.

revealed to current designations of threats to mammalian species from the 1996 IUCN Red List of Threatened Animals (IUCN, 1997). The IUCN Red List contained 460 of the species in our data set, and 416 of these species at risk to extinction in the wild, though the degree of threat may vary (Table 6). Nine additional species were listed as extinct or extinct in the wild. The remaining listed species were of concern because they are little known (viz., data deficient). Listed species exhibited very strong overlap with our rarest category (about 81% of category H species were listed), and also some overlap with cells that contained species with relatively low population densities (about 70% of the species were listed).

DISCUSSION

Extreme rarity in mammals?

Among the species of mammals in our data set, a strong bimodal pattern was evident of more very common and very rare species than would be expected at random (cells A and H, Figs 1 and 2; Table 1). For Orders of mammals with more than about forty species sampled, however, virtually all forms of rarity were represented. Cells in the rarity model that had the least species compared to expectations were those with relatively large range areas and low local population densities (cells C and D), and relatively small ranges and high densities (cells E and F). Only a little over one-quarter of the global mammalian fauna was examined, however, so these patterns should be viewed cautiously.

Table 2 Percentage of species in cell H (Fig. 1) of each Order of mammals (Orders with less than ten species examined not shown)

Order*	No. of species examined	No. of species in cell H	Percentage of species in cell H	χ^2
Perissodactyla	12	9	75.0	11.5**
Diprotodontia	73	25	34.2	1.5
Insectivora	208	70	33.7	4.5
Primates	60	19	31.7	0.4
Carnivora	196	62	31.6	1.8
Dasyuromorphia	52	13	25.0	0.1
Lagomorpha	78	19	24.4	0.3
Rodentia	255	60	23.5	2.0
Artiodactyla	47	10	21.3	0.6
Scandentia	19	4	21.1	0.1
Cetacea	15	3	20.0	0.1
Chiroptera	158	28	17.7	8.1
Total	1173	322	27.5	33.3***

*Orders not included due to small sample sizes: Didelphimorpha (8 species), Xenarthra (2), Hyracoidea (2), Macroscelidea (2), Microbiotheria (1), Monotremata (2), Notoryctemorpha (1), Paucituberculata (1), Peramelemorphia (8), Pholidota (3), Polyprotodontia (1), Proboscidea (2), Sirenia (5), Tubulidentata (1).
**Post hoc pair-wise χ^2 tests, $\alpha' = 0.004$, $\chi^2_{0.004} = 9.2$ (d.f. = 1).
***Test of homogeneity for entire table, $\chi^2_{0.05} = 19.7$ (d.f. = 11).

Table 3 The mean rank of rarity for Orders of mammals (Orders with less than ten species not shown, see Table 2). Probability levels from paired Mann–Whitney *U*-tests (each Order compared post hoc pair-wise to the rest of the species, $\alpha' = 0.004$).

Orders	*N*	Mean rank	*P*
Perissodactyla	12	1.42	0.001
Primates	60	2.03	0.001
Diprotodontia	71	2.17	0.001
Carnivora	196	2.28	0.001
Cetacea	15	2.33	0.48
Dasyuromorphia	52	2.37	0.61
Lagomorpha	78	2.47	0.74
Insectivora	208	2.58	0.35
Rodentia	255	2.59	0.30
Artiodactyla	47	2.62	0.54
Scandentia	19	2.63	0.71
Chiroptera	158	2.87	0.001
Total	1212*	2.50*	

*Values for all species, including Orders with less than ten species.

Table 4 Numbers of species examined in each Order of mammals (Orders with less than ten species not shown, see Table 2).

Orders	Total no. of species*	No. of species examined	Percentage of species examined	χ^2 value
Rodentia	1793	255	14.2	287.5**
Chiroptera	977	158	16.2	86.9**
Cetacea	77	15	19.5	2.4
Artiodactyla	194	47	24.2	1.3
Primates	201	60	29.9	0.3
Insectivora	365	208	57.0	263.8**
Diprotodontia	116	71	61.2	63.5**
Perissodactyla	16	12	75.0	15.3**
Dasyuromorphia	63	52	82.5	91.5**
Carnivora	235	196	83.4	375.0**
Lagomorpha	78	78	100.0	200.5**
Scandentia	19	19	100.0	45.5**
Total	4327*	1212	28.0	1334.1***

*Number of species from Corbet & Hill (1991) and Wilson & Reeder (1993).
**Post hoc pair-wise χ^2 tests, $\alpha' = 0.004$, $\chi^2_{0.004} = 9.2$ (d.f. = 1).
***Test of homogeneity for entire table, $\chi^2_{0.05} = 19.7$ (d.f. = 11).

Table 5 Number of species examined in each zoogeographic region. Marine species and species in transitional zones are not included (* in parentheses are the numbers of included species with relatively poor data).

	Biogeographic region[a]						
Rarity cell	PA	NA	NT	AT	IM	AA	Total
A	80	100(11*)	65(9*)	25(1*)	35(2*)	62	367
B	27(1*)	51(9*)	17(4*)	10(1*)	31(1*)	17	153
C	5	16(3*)	18(4*)	12(1*)	5(2*)	9	65
D	15(1*)	21(1*)	20(6*)	13	17(4*)	16	102
E	4	17	2(1*)	4	9(1*)	21	57
F	10	29(6*)	5(2*)	9	13(1*)	38	104
G	4	5(2*)	4	22	7	13	55
H	38	36(8*)	46(13*)	36(2*)	79(4*)	65	300
No. examined	183	275	177	131	196	241	1203
No. world spp.	475	356	937	868	792	440	3868
% examined[b]	38.5[c]	77.2[c]	18.9[c]	15.1[c]	24.7[c]	54.8[c]	31.1
% in cell H[d]	20.8	13.1[e]	26.0	27.5	40.3[e]	27.0	24.9

[a]PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; IM, Indomalayan; AA, Australasian.
[b]Test of homogeneity: $\chi^2 = 754.8$ (d.f. = 5), $P < 0.0001$.
[c]Post hoc pair-wise χ^2 tests, $\alpha' = 0.01$, $\chi^2_{0.01} = 7.3$ (d.f. = 1), $P < 0.01$.
[d]test of homogeneity: $\chi^2 = 48.1$ (d.f. = 5), $P < 0.0001$.
[e]post hoc pair-wise χ^2 tests, $\alpha' = 0.01$, $\chi^2_{0.01} = 7.3$ (d.f. = 1), $P < 0.01$.

Table 6 Classifications of our sample of the mammalian species by the 1996 IUCN Red List of Threatened Animals.

	IUCN Categories*									
Rarity cell	EX	EW	CR	EN	VU	LR	DD	IUCN listed	Rarity sample	Percent listed
A				1	5	11	1	18	317	5.7
B				1	5	6	3	15	178	8.4
C				3	5	10	1	19	58	32.8
D				6	18	18	8	50	99	50.5
E				2	6	6	2	16	61	26.2
F			1	2	7	18	1	29	108	26.9
G			2	12	16	12	3	45	60	75.0
H	7	2	33	85	73	52	16	268	331	81.0
Total	7	2	36	112	135	133	35	460	1212	38.0

* EX, extinct; EW, extinct in the wild; CR, critically endangered; EN, endangered; VU, Vulnerable; LR, lower risk; DD, data deficient.

The IUCN's Red List of mammals classifies about one-fourth of the mammalian species as deserving conservation concern (IUCN, 1997). IUCN criteria for listing rely heavily on temporal changes in species, such as recent declines in population numbers (IUCN, 1994). Our classification of rarity draws from static data on current species status, and thus contains a somewhat different basis of classification (Dobson *et al*., 1997). These two complementary evaluations of current status both indicate rarity among about one-fourth of the world's mammals. Our somewhat independent analyses supports the IUCN's designation of high degrees of threat to about one-fourth of the mammals. Our category with the rarest species, however, contained sixty-three species that were not listed by the IUCN (Appendix, which does not include fifteen species in category H that were classified by the IUCN as 'data deficient'). In general, these are species about which little is known. Such species should be studied and evaluated to determine their true conservation status (Caughley, 1994).

Brown (1984, 1995) provides a 'niche-based' hypothesis to explain bimodal patterns in taxa that exhibit high degrees of both commonness or rarity. His reasoning was basically that generalist species should be widespread and abundant because of the environmental flexibility that generalization entails. Specialists, on the other hand, should be rare because the conditions necessary for their existence will be widely separated and thinly spread in nature. From Brown's (1995) hypothesis, we would expect many species to fall into the rarest and most common categories in the 7 forms of rarity model. From the IUCN's findings (discussed above), we might have expected about one-fourth of the species to be relatively rare. Thus, our classifying about one-fourth of the species in the most extreme category of rarity might not provide a proper *a priori* test of the niche-based hypothesis. The high proportion of species in the most common category, however, lends stronger support for the niche-based hypothesis. It should also be noted that this is a macroecological generalization to which there are many exceptions.

The influence of Orders

Some Orders, particularly those that contain fairly large mammals, appeared to contain high proportions of rare species. Although only perissodactyls had a significantly high proportion of species in the relatively rarest category (Table 2), the ranking procedure indicated that primates, carnivores, and diprotodonts also exhibited relatively higher degrees of rarity among their species than other Orders of mammals (Table 3). Fairly large samples of the species of these Orders were available (Table 4), so general conservation concern about them seems justified. This conclusion has been reached for some of these Orders in pervious studies on Neotropical forest mammals (Arita *et al*., 1990; Dobson & Yu, 1993) and the global mammalian fauna (Cole *et al*., 1994). Cole *et al.* (1994) also indicated that the mammalian Orders Cetacea, Proboscidea, and Sirenia should receive immediate conservation efforts. These latter groups of large mammals were not sufficiently sampled in our data set to evaluate their relative rarity (Table 2).

On the other hand, Ceballos & Brown (1995) argue that the majority of species that are threatened are rodents and bats, simply because these taxa have many species (Table 4). When considered on a proportional basis, however, rodents and bats have relatively low frequencies of rare species (Ceballos & Brown, 1995; IUCN, 1997; Table 3). The question is whether the conservation of each species is valued equally, or whether groups should be targeted for conservation on a relative basis. Regardless of this decision, however, the results likely suffer from sampling biases. Many studies of rodents appeared to focus on North American species that were relatively common (see below). In addition, bats can have very large ranges in which such critical resources as hibernacula might be relatively concentrated and uncommon. A further source of bias was that Orders were not sampled evenly in our data set, with significantly low proportions of the species of rodents and bats represented (Table 4).

Zoogeography of rarity

Tropical zoogeographic regions might be expected to have the greatest numbers of rare species, simply because they contain absolutely more species than temperate regions (Table 5). In fact, zoogeographic regions that contained large tropical regions all exhibited greater than average proportions of species in the relatively rarest category, a result that was statistically significant for the Indomalayan region. Our data sources, however, exhibited a strong sampling bias. The Nearctic fauna was strongly represented with over three quarters of the species sampled. Other zoogeographic regions, with the exception of continental Australia (Strathan, 1995), were under-sampled by comparison. For example, less than a sixth of the Afrotropical fauna occurred in the sample. This bias occurred in part because many of the data came from the Species Accounts publication series of the American Society of Mammalogists, which naturally emphasized North American species. In general, temperate zoogeographic regions were better represented than the tropics.

A second contribution to bias in sampling of zoogeographic regions was the haphazard nature of reporting of biological characteristics of species listed in IUCN documents. For example, the IUCN documents on lagomorphs and cats provide species accounts with density, range, and habitat data for all or most of the species in these groups, whether relatively rare or common (Chapman & Flux, 1990; Nowell & Jackson, 1996). Similar extensive works for Australia presented suitable information for us to include a large proportion of the continental fauna of both relatively rare and common species (Kennedy, 1992; Strathan, 1995). As more IUCN reports are issued, estimates of both rarity and threat to the global mammalian fauna will improve in accuracy. In particular, the Afrotropical region exhibits high levels of endemism that should indicate a high proportion of relatively rare species (Cole *et al*., 1994). A detailed review of the Afrotropical region is clearly warranted.

Comparison of rarity and threats to species

Of the 1212 species that we examined, 460 (38.0%) were listed in the 1996 IUCN Red List of Threatened Animals (Table 6). Nine species were extinct or extinct in the wild, and a further thirty-five did not have sufficient data for IUCN assignment. Thus, 34.3% (416/1212) of our remaining species were listed as threatened, a higher proportion than among mammals in general (IUCN, 1996). This result likely reflects our use of IUCN documents on groups of species that contain high proportions of rare species. The bulk of our IUCN listed species (83.0%) fell into forms of rarity that included relatively low population densities (cells C, D, G, and H; Fig. 1), reflecting the reliance of the IUCN listing criteria on declines in population size (IUCN, 1994). Most IUCN listed species (85.2%) fell into categories of relative rarity in two or three variables of the 7 forms or rarity model (viz., cells D, F, G, and H). It is important to note that when populations experience abrupt declines, relatively common species can be classified as threatened (e.g. eighteen IUCN-listed species were in cell A).

CONCLUSION

As a group, mammalian species exhibit a strong bimodal pattern of many relatively common and rare species. This pattern, plus the exceptionally high proportion of mammalian species listed as threatened by the IUCN (1996), suggests that many mammals exhibit a strong tendency towards rarity. Brown's (1995) niche-based hypothesis appears to explain this pattern well, but there are also species that exhibit characteristics of all forms of rarity. In the readily available literature, there are strong biases that need to be addressed. Orders of smaller mammals have not been adequately sampled (see also Ceballos & Brown, 1995). Most zoogeographic regions outside of North America and Australia do not have easily available quantitative data on basic characteristics of their species, especially the tropical regions. New IUCN studies, however, may be expected to remediate this problem. Finally, although static studies of rarity can aid us in identifying taxa that warrant further conservation study, temporal studies of change in characteristics of species should prove most helpful in determining threats to mammalian species (Caughley, 1994; Dobson *et al*., 1995; Dobson *et al*., 1997).

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Appendix. Species from cell H of our analysis of mammalian rarity that were not listed in any category by the IUCN (1997). Nomenclatural authorities may be found in Wilson & Reeder, 1993).

Order	Genus and species
Artiodactyla	*Ovibos moschatus*
Carnivora	*Bassaricyon alleni*
Carnivora	*Crossarchus ansorgei*
Carnivora	*Cynogale lowei*
Carnivora	*Felis nigripes*
Carnivora	*Genetta victoriae*
Carnivora	*Mologale orientalis*
Carnivora	*Neophoca cinerea*
Carnivora	*Paradoxurus lignicolor*
Carnivora	*Profelis aurata*
Carnivora	*Proteles cristatus*
Carnivora	*Spilogale pygmaea*
Cetacea	*Phocoena dioptrica*
Chiroptera	*Erophylla sezekorni*
Chiroptera	*Mormopterus norfolkensis*
Chiroptera	*Natalus micropus*
Chiroptera	*Pteropus* (unnamed species)*
Chiroptera	*Scoteanax rueppelli*
Chiroptera	*Scotorepens orion*
Chiroptera	*Vespadellus douglasorum*
Dasyuromorphia	*Ningaui yvonneae*
Dasyuromorphia	*Pseudantechinus ningbing*
Dasyuromorphia	*Sminthopsis virgniae*
Diprotodontia	*Cercartetus lepidus*
Insectivora	*Cryptotis magna*
Insectivora	*Hemiechinus nudiventris*
Insectivora	*Sorex ornatus*
Insectivora	*Sorex tenellus*
Lagomorpha	*Lepus melainus*
Lagomorpha	*Ochotona erythrotis*
Lagomorpha	*Ochotona gloveri*
Lagomorpha	*Ochotona ladacensis*
Perissodactyla	*Equus kiang*
Primates	*Presbytis johnii*
Rodentia	*Ammospermophilus harrisii*
Rodentia	*Ammospermophilus insularis*
Rodentia	*Arborimus longicaudus*
Rodentia	*Chaetodipus lineatus*
Rodentia	*Dipodomys elephantinus*
Rodentia	*Dipodomys nelsoni*
Rodentia	*Geomys arenarius*
Rodentia	*Neotoma goldmani*
Rodentia	*Peromyscus alstoni*
Rodentia	*Peromyscus stirtoni*
Rodentia	*Phenacomys albipes*
Rodentia	*Proechimys iheringi*
Rodentia	*Reithrodontomys creper*
Rodentia	*Reithrodontomys tenuirostris*
Chiroptera	*Ectophylla alba***
Chiroptera	*Glossophaga mexicana***
Chiroptera	*Natalus major***
Insectivora	*Cryptotis goodwini***
Insectivora	*Sorex bendirii***
Insectivora	*Sorex gaspensis***
Insectivora	*Sorex pacificus***
Lagomorpha	*Ochotona himalayana***
Rodentia	*Dipodomys compactus***
Rodentia	*Microtus breweri***
Rodentia	*Neotoma stephensi***
Rodentia	*Proechimys dimidiatus***
Rodentia	*Reithrodontomys brevirostris***
Rodentia	*Tamias bulleri***
Rodentia	*Tamias durangae***

*The Torresian flying-fox (see Strathan, 1995).
**Species with relatively poor data (see text).