Effects of Human Activity on Global Extinction Risk

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Abstract: *Both natural and anthropogenic factors are important in determining a species' risk of extinction. Little work has been done, however, to quantify the magnitude of current anthropogenic influences on the extinction process. The purpose of this study is to determine the extent to which measures of the intensity of human activity are related to the global variability of two measures of species' susceptibility to extinction. We observed six indices of human activities in 90 countries, and we tested their relationships to the proportion of threatened bird and mammal species in each country, as well as to mammalian population density. After correcting for area effects, latitudinal diversity gradients, and body size (for population density), 28 to 50% of the remaining variation was statistically attributable to anthropogenic variables. Different measures of anthropogenic influence were most closely related to extinction risk in birds and mammals. Human population density was the variable most closely related to the proportion of threatened bird species per country, whereas per capita GNP was more important for mammal species. Mammalian population density strongly correlates with the extent of protected area per country. Contrary to suggestions in earlier literature, our work does not support the hypothesis that habitat loss is a prime contributor to species loss because frequencies of threatened birds and mammals are not closely related to patterns of land use.*

Efectos de la actividad humana sobre el riesgo de extinción global

Resumen: *Tanto los factores naturales como los antropogénicos son importantes en la determinación del riesgo de extinción de una especie. Sin embargo, se han llevado a cabo pocos estudios para cuantificar la magnitud de las influencias antropogénicas actuales sobre el proceso de extinción. El propósito de este estudio es determinar hasta que grado las medidas de intensidad de las actividades humanas están relacionadas con la variabilidad global de dos medidas de susceptibilidad de una especie a la extinción. Se observaron seis índices de actividades humanas en 90 paises, y se examinaron sus relaciones con la proporción de especies de aves y mamíferos amenazados en cada país asi como con la densidad de las poblaciones de mamíferos. De corregir los efectos del área, de los gradientes de diversidad latitudinales y del tamaño corporal (para la densidad poblacional), un 28-50% de la variación remanente fue estadísticamente asi como artribuíble a variables antropogénicas. Diferentes medidas de influencias antropogénicas estuvieron estrechamente relacionadas con el riesgo de extinción en aves y mamíferos. La densidad poblacional humana fue la variable que estuvo más estrechamente relacionada con la proporción de especies de aves en peligro por pais y el PBI per capita fue más importante para las especies de mamíferos. La densidad poblacional de mamíferos se correlaciona fuertemente con la extensión del área protegida por pais. En forma opuesta a lo sugerido en estudios anteriores, nuestro trabajo no sustenta la hipótesis de que la pérdida de hábitat es uno de los principales contribuyentes a la pérdida de especies, debido a que la fracción de aves y mamíferos en peligro no está estrechamente relacionada con los patrones de uso de la tierra.*

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Paper submitted April 25, 1994; revised manuscript accepted December 27, 1994.

Introduction

Every continental extinction in recorded history has been attributed to human activities (Soulé 1983; Diamond 1986). Factors such as habitat degradation, hunting, competition with introduced species, and pollution have been implicated in the decline of natural populations in the past. Although it might be desirable to limit such activities to reduce the risk of future extinctions, this presents two problems. First, the socioeconomic consequences of doing so could be severe. Second, the human activities that most severely threaten species' survival today are not necessarily the same as those that have been responsible for extinctions historically. It would therefore be worthwhile to attempt to identify which current human activities most strongly increase the risk of species extinctions, a subject that has received very little attention to date (di Castri & Younes 1990).

Future risk of extinction might be assessed by evaluating species' population sizes or densities, both of which have been related to risk of species extinction (Shaffer 1987; Kattan 1992). Species currently or potentially susceptible to extinction, such as those whose populations are small, are often classified as threatened. If particular human activities were responsible for the reduction of natural populations to threatened levels, then one would expect that, in regions with high levels of those activities, the proportion of threatened species would be higher. Similarly, natural populations in such areas should have lower than average population densities.

The specific human activities that lead to the local reduction of natural populations vary tremendously, depending on which species and which areas of the world are examined (Sala 1992). The ultimate causes of human-induced extinctions are likely to be socioeconomic in origin (Myers 1988; Wilson 1988; Gullison & Losos 1993). To formulate a global response to the loss of species richness, it would be useful to identify which socioeconomic factors are commonly associated with high risk of extinction among species in general (Kassas 1989; Lubchenco et al. 1991).

The purpose of this study was to examine the correlations between classes of human activities, as measured by common socioeconomic variables, and indices of extinction risk among birds and mammals (hypotheses summarized in Table 1). We focused on these two groups because their taxonomy is relatively well known (Soulé 1990) and their status closely monitored. There were two components to this study. We first examined the numbers of threatened bird and mammal species in about 90 countries in order to quantify their relationships to several common socioeconomic indicators. Second, we related mean mammalian population density to the same indicators.

Among the anthropogenic factors thought to be related to extinction rates is poverty (Raven 1988), which can be measured by per capita GNP. Poverty has been observed to lead to increased birth rates (Murdoch 1983) and unsustainable exploitation of resources. Increased reliance on subsistence hunting, one of the consequences of poverty (World Resources Institute 1992), has been implicated in the decline of many animal, especially mammal, populations (Redford 1992).

A second factor associated with biodiversity loss is human overpopulation (Lovejoy 1988). As the human population rises a greater proportion of net primary productivity is appropriated by humans. It is estimated that nearly 40% of all net terrestrial primary productivity is now used by humans and is unavailable to other species (Vitousek et al. 1986). This is accompanied by extensive loss of natural habitat. It has been suggested that such losses increase the likelihood of massive extinction, possibly leading to a 50% reduction of global species richness by 2050 (Ehrlich & Ehrlich 1992).

Several other anthropogenic factors are widely thought to be related to extinction risk. Human birth rates provide a measurement of socioeconomic status, which is related to many facets of environmental degradation (World Resources Institute 1992). Similarly, the

Table 1. Factors hypothesized to influence susceptibility to extinction among birds and mammals.

Factor	*Rationale*
Human population	High populations lead to habitat loss that increases numbers of threatened species and to reduced population densities.
Per capita GNP	Subsistence hunting and uncontrolled sport hunting and poaching are more extensive in poorer countries, and damaging land use practices are less likely to be regulated.
Extent of protected area	Protected areas may be established to safeguard threatened species, and they may permit higher population densities.
Total cropland	Loss of habitat attributable to agricultural activity increases numbers of threatened species and reduces population densities.
Birth rates	High birth rates are related to poor socioeconomic conditions.
Per capita industrial CO_2 emissions	Greater industrialization may result in higher pollution levels.

extent of crop land per country may reflect habitat loss that can render natural populations susceptible to extinction. Pollution, also a central issue in the decline of species richness, is a problem most closely associated with industrialized areas (Barker & Tingey 1992). Therefore, measurements of industrialization, such as per capita industrial CO_2 emissions, may be related to species' likelihood of extinction.

Reserve systems may reduce biodiversity loss (Diamond 1975) by maintaining significant areas of habitat relatively free from anthropogenic disturbance. If the reserves are effective, then there should be an inverse relation between extent of protected area and extinction risk, as measured by numbers of threatened species and population density.

Methods

Data for the socioeconomic variables listed in Table 1, as well as the numbers of species of threatened mammals and birds, were extracted from a large statistical database assembled by the World Resources Institute (DSC Data Services 1992). Numbers of threatened mammal species per country were available for 82 countries world-wide. Similarly, numbers of threatened bird species in 95 countries were available. Threatened species lists were assembled by the World Conservation Union Species Survival Commission, the International Council for Bird Preservation, and the World Conservation Monitoring Centre. These data were used to test the hypothesis that some of the variance in numbers of threatened species per country is related to the anthropogenic variables listed in Table 1. While these data may not be complete for every country included in our samples, they are the most thorough compilation available.

The number of threatened species per country is also likely to covary strongly with the total number of species per country (total species richness). Because we are specifically interested in the anthropogenic correlates of the number of threatened species per country, it was necessary to first control for the non-anthropogenic factors that influence total species richness. Most notably, total richness depends upon the area sampled and upon geographic location (Wilson 1992). To control for these non-anthropogenic factors, partial correlations between the number of threatened species and anthropogenic variables were calculated after controlling for total bird or mammalian species richness and land area per country. This eliminated the effect that latitude or country size may have had on the variables: diversity estimates from large or tropical countries became comparable to those from small or high-latitude countries. Note that the partial correlations change the interpretation of the variables. For example, the total human population per country, when controlled for area, becomes equivalent to human population density. The number of threatened species per country, controlled for total richness, becomes the proportion of species that are threatened, and so on.

We square-root-transformed the number of threatened bird and mammal species (the dependent variables) in order to stabilize their variances when regressed against socioeconomic indicators. Socioeconomic variables were transformed, where necessary, to linearize their relationships with the transformed numbers of threatened species. In cases where relationships remained significantly nonlinear, polynomial regressions were used. When multiple regression models were constructed, all possible subsets were examined to identify the best model.

After determining which anthropogenic variables correlate with the proportion of threatened species per country, one can then test, using path analysis, hypothesized causal relationships among anthropogenic factors and the proportion of threatened species. Based on the hypothesized model structure on can derive predictions about the expected simple and partial correlations. For example, if X determines Y, which in turn determines Z, then the correlation between X and Z cannot be stronger than the correlations between X and Y or between Y and Z. The best path-analysis models were selected based on agreement between predicted and observed correlations (Sokal & Rohlf 1981). To remove the effects of non-anthropogenic factors from the path analyses, we used the partial correlations among variables, holding constant total species richness and land area per country. Note that, although one can reject causal hypotheses using path analysis, one cannot prove the existence of causal relationships; one can only identify causal frameworks that are consistent with the observed correlations. Among these causal frameworks it is still possible that intermediate variables or indirect relationships can affect the observed correlations.

A similar procedure was performed to analyze the dependence of mammalian population density on anthropogenic variables. Data on mammalian population densities and body size were collected from the biological literature by Currie and Fritz (1993). To these we have added a few more recently published observations. Density data that were not taken from industrialized countries were taken from approximately the same period as the socioeconomic data (1988–1991). Data from industrialized countries over a wider time window (up to 30 years prior to the socioeconomic data) were included in our analyses because we felt it safe to assume that socioeconomic conditions have been relatively stable in industrialized countries throughout this period. Population density observations are derived from local measurements and do not represent the density of the mammal population over its entire range. Seventy-eight density and mass values were obtained from nine different countries. For each of those countries data for the anthropogenic variables hypothesized in Table 1 were then collected from the World Resources Database. These data were used to test the hypothesis that some of the variance in mammalian population density is related to the anthropogenic variables.

Average population density varies with body size (Currie & Fritz 1993). In order to render population density data comparable for organisms of different mass, partial correlation coefficients between density and the socioeconomic variables were calculated after adjusting for body size. Population density, after individual body size is controlled for, can be regarded as the extent to which a species is more or less abundant than other species of comparable body mass. A multiple regression analysis was then performed, and the best model was chosen from among all subsets regression. Path analysis was used to investigate the causal relationships among variables. In the path analyses the effect of mammalian body size and land area were first statistically controlled by the use of partial correlations. We then included all socioeconomic variables that were correlated with mammalian population density in the path models. Note that these variables need not be the same as those included in the path models that deal with the numbers of threatened species.

Results

Threatened Species per Country

The number of threatened bird species per country is strongly related to several socioeconomic variables. This is due, at least partly, to covariation with total bird species richness and land area per country (Table 2). After these two influences are controlled for (Table 3), the proportion of threatened bird species per country remains strongly related to the total human population (Fig. 1) and to human per capita birth rates (Fig. 2). The multiple regression model that explains the greatest amount of variation in the number of threatened bird species per country incorporates these two variables as well as total bird richness and land area per country ($R^2 = 0.81$, $p < 0.0001$, $n = 95$; Table 4). If the influence of the non-anthropogenic variables is removed, then human population and per capita birth rates per country explain 42% of the residual variability in numbers of threatened bird species per country (Table 4). Other measures of anthropogenic activity also show significant partial correlations with threatened bird species per country (Table 3), but these variables are not significant after human population and birth rates per country are accounted for.

Similarly, numbers of threatened mammal species are also related to most of the anthropogenic variables. Land area, total mammalian richness, and per capita GNP show the strongest relationships with numbers of threatened mammal species per country ($R^2 = 0.72$, $p < 0.0001$; Table 4). When the effects of land area and mammal richness are held constant, per capital GNP remains the strongest correlate of proportions of threat-

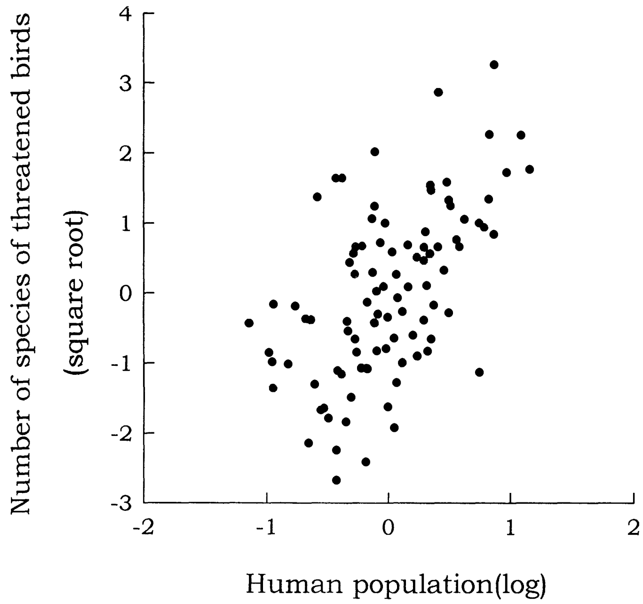

Figure 1. Partial plot of numbers of threatened bird species per country against human population per country. The effects of land area and bird species richness per country have been statistically controlled.

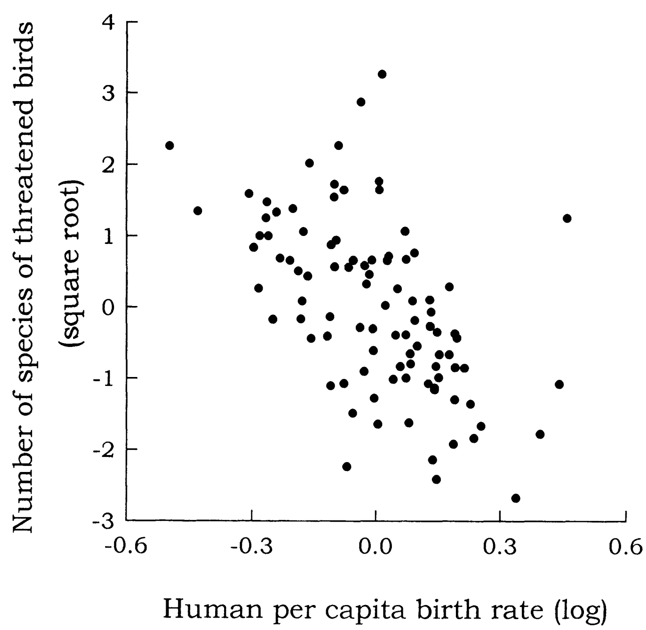

Figure 2. Partial plot of numbers of threatened bird species per country against birth rates per country. The effects of land area, bird species richness per country, and bird species richness (square root transformed) have been statistically controlled.

Table 2. Simple Pearson correlations between indices of extinction risk, the major non-anthropogenic covariates of extinction risk, and several socioeconomic measures of anthropogenic activity.[a]

	Indices of susceptibility to extinction			Non-anthropogenic covariates		
Factor	*Threatened bird species (square root; 9.0* n = 95*)*	*Threatened mammal species (square root;* n = 82*)*	*Mammalian population density (log;* n = 78*)*	*Land area (log;* n = 78 to 95*)*	*Total bird species richness (square root;* n = 95*)*	*Total mammal species richness (square root;* n = 82*)*
Land area (log)	0.56[b]	0.60[b]	NS	—	0.59[b]	0.64[b]
Body size (log)	—	—	−0.68[b]	NS	—	—
Human population (log)	0.71[b]	0.43[b]	−0.45[b]	0.70[b]	0.47[b]	0.52[b]
Per capita GNP (log)	NS	−0.50[b]	0.68[b]	NS	−0.38[c]	−0.31[c]
Extent of protected area (log)	NS	NS	0.75[b]	NS	NS	0.60[b]
Total cropland (log)	0.63[b]	0.47[b]	−0.25[c]	0.78[b]	0.46[b]	0.54[b]
Birth rates (log)	−0.32[c]	0.46[b]	−0.60[b]	NS	0.36[c]	0.30[c]
Per capita industrial CO_2 emissions (log)	0.27[c]	−0.32[c]	NS	NS	NS	NS
Total bird species richness (square (root)	0.72[d]	—	—			
Total mammal species richness (square root)	—	0.77[b]	—			

[a] With the exception of individual body mass, each of the variables above was measured at the level of individual countries. In cases where variables have been transformed before analysis, the transformation is indicated in parentheses after the variable name. NS $p > 0.05$.
[b] $p < 0.0001$.
[c] $p < 0.01$.
[d] $p < 0.0001$. R^2 for a second-degree polynomial relation.

ened mammal species per country (partial $R^2 = 0.28$, $p < 0.0001$; Fig. 3 and Table 4). Partial correlations with industrial CO_2 emissions and birth rates per country are significant after land area and total mammal species richness per country are controlled for, but not after per capita GNP per country is controlled for as well.

Curiously, there is no significant relationship between numbers of threatened mammal and bird species per country after land area and species richness per country are adjusted for ($r = 0.02$, $p = 0.83$, $n = 96$). In other words, the countries in which a high proportion of bird species are threatened are not the same as those in

Table 3. Partial correlations between indices of susceptibility to extinction and measures of anthropogenic activity after controlling for land area and bird or mammal diversity per country (threatened species columns) or body size (population density column).[a]

Factor	*Threatened bird species (square root; $n = 95$)*	*Threatened mammal species (square root; $n = 82$)*	*Mammalian population density (log; $n = 78$)*
Human population	0.56[b]	NS	−0.51[b]
Per capita GNP	0.35[c]	−0.53[b]	0.44[b]
Extent of protected area	NS	NS	0.66[b]
Total cropland	0.46[b]	NS	0.38[c]
Birth rates	−0.55[b]	0.49[b]	−0.25[c]
Per capita industrial CO_2 emissions	0.36[c]	−0.40[c]	NS

[a] In cases where variables have been transformed before analysis, the transformation is indicated in parentheses after the variable name. (NS $p > 0.05$).
[b] $p < 0.001$.
[c] $p < 0.05$.

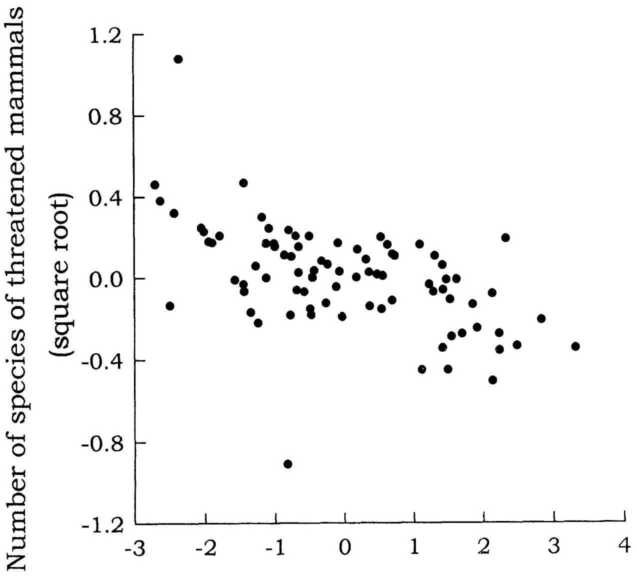

Figure 3. Partial plot of numbers of threatened mammal species per country versus per capita GNP per country. The effects of land area and mammal species richness per country have been statistically controlled.

which a high proportion of mammal species are threatened (Table 5). Presumably, therefore, the factors that cause mammals and birds to become threatened also differ.

Mammalian Population Density

Mammalian population density is also related to several anthropogenic variables. Extent of park land, per capita GNP, land area, and body size are strongly related to mammalian population density ($R^2 = 0.77, p < 0.0001$, Table 4). After body size was statistically controlled in order to correct for the mass-density relationship (Currie & Fritz 1993), the extent of park land and per capita GNP remain strongly related to mammalian population density (partial $R^2 = 0.50, p < 0.0001, n = 78$; Table 4). Both regressors show a monotonic, increasing relationship with mammalian population density (Figs. 4 and 5).

Path Analysis

We used path analysis models to test structural interpretations—which variables most directly influence each other—of the partial correlations calculated above. Because a large number of variables are correlated with the indices of extinction risk, there is a large number of ways in which those variables might interact. Consequently, there are many possible path models, more than one of which are consistent with the data. In each of the following cases we present only the model that showed the best agreement between predicted and observed partial correlations, even though there were a small number of alternative models that were also consistent with the data. These alternatives were generally similar to the mod-

Table 4. Regression models predicting numbers of threatened bird and mammal species per country and mammalian population density.*

Dependent variable	*Model*	R^2
Threatened bird species (square root)	7.10	0.81
	−0.504 total bird richness	
	+0.013 total bird richness (square root)	
	+0.163 land area (log)	
	+0.961 total human population (log)	
	−2.63 birth rates (log)	
Threatened bird species (square root)	0.00	0.42
adjusted for land area (log), and total bird richness	+0.961 total human population (log)	
	−2.63 birth rates (log)	
Threatened mammal species (square root)	+1.31	0.71
	+0.00991 total mammal richness (square root)	
	+0.00141 total mammal richness	
	+0.170 land area (log)	
	−0.096 per capita GNP (log)	
Threatened mammal species (square root)	0.00	0.28
adjusted for land area (log), and total mammal richness	−0.096 per capita GNP (log)	
Mammalian population density (log)	−2.61	0.77
	+1.06 per capita GNP (log)	
	+2.82 extent of protected land (log)	
	−0.36 body size (log)	
	−0.61 land area (log)	
Mammalian population density (log)	0.00	0.50
adjusted for body size (log)	+1.06 per capita GNP (log)	
	+2.82 extent of protected land (log)	

**In cases where variables have been transformed before analysis, the transformation is indicated in parentheses after the variable name. All models are significant at $p < 0.0001$.*

Table 5. The countries in the present data set with the lowest and the highest percentages of threatened birds and mammals.

Country	Threatened birds (%)	Country	Threatened mammals (%)
Malawi	0.2	Central African Republic	0.48
Benin	0.2	Trinidad & Tobago	1.18
Burkina Faso	0.2	New Zealand	1.45
Gambia, The	0.2	Sweden	1.54
Niger	0.2	Denmark	2.04
Central African Rep	0.3	Germany, Federal Republic	2.13
El Salvador	0.5	Swaziland	2.17
Guinea-Bissau	0.5	Austria	2.35
Congo	0.6	Canada	2.54
Mali	0.6	United Kingdom	2.6
China	6.9	India	11.1
Ireland	7.2	Niger	11.5
Philippines	7.2	Mali	11.8
Switzerland	7.6	Algeria	12.4
Brazil	7.9	Philippines	12.5
Denmark	8.4	Chad	13.7
Indonesia	9	Comoros	17.6
New Zealand	9.2	Jamaica	20.7
United Kingdom	9.4	Mauritania	23
Madagascar	11	Madagascar	50.5

els we present, usually differing in the direction of a postulated interaction among the anthropogenic variables (for example, *A* influences *B*, versus *B* influences *A*).

The numbers of threatened bird species per country is most directly related to human population and per capita birth rates (Fig. 6). Per capita GNP and industrial CO_2 emissions apparently influence birds only indirectly, through their effects on birth rates. The relationships among industrialization, GNP, and birth rates are consistent with notion of demographic transition (Murdoch 1983): increasing industrialization leads to increased wealth (GNP), which leads to decreased birth rates. The decreased birth rates are, in turn, related to greater proportions of threatened bird species.

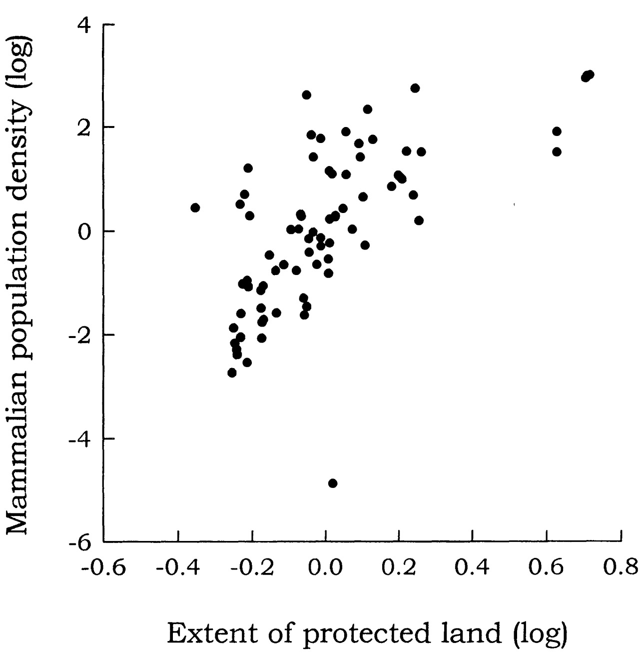

Figure 4. Partial plot of mammalian population density versus extent of park land. The effects of body size have been statistically controlled.

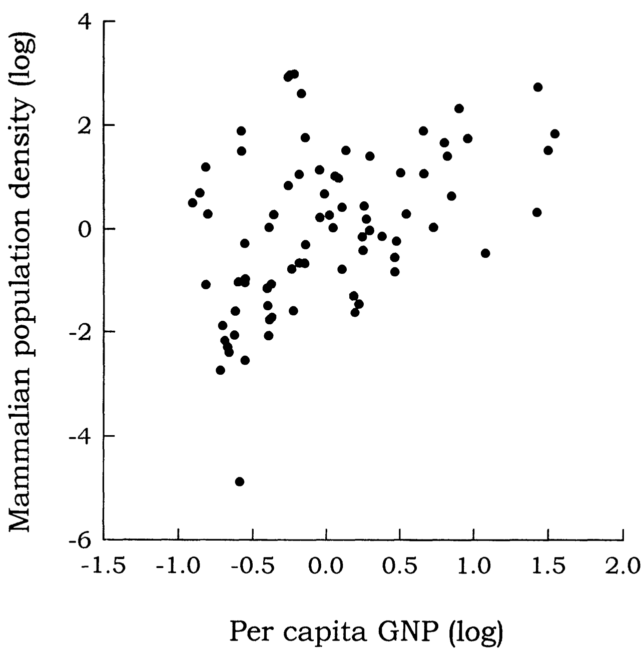

Figure 5. Partial plot of mammalian population density versus per capita GNP. The effects of body size have been statistically controlled.

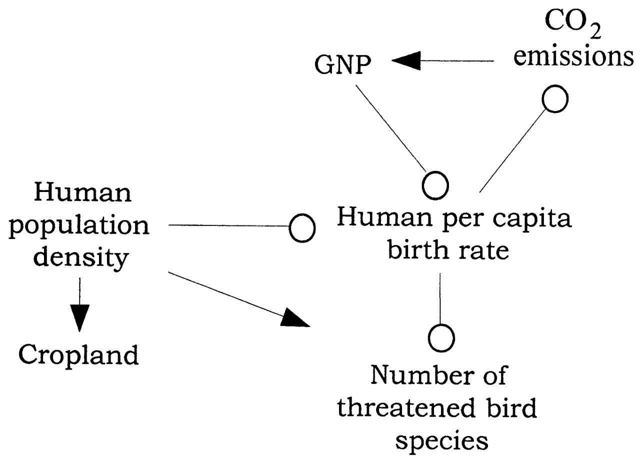

Figure 6. Path analysis diagram of the factors influencing the numbers of threatened bird species per country (square-root transformed). An arrow from one factor to another indicates that the correlations are consistent with the hypothesis that the first variable directly influences the second (although other unobserved variables may intervene). A solid triangular head indicates a positive influence; an open circular head indicates a negative influence.

In contrast, the number of threatened mammal species per country was most directly related to per capita GNP (Fig. 7). Although per capita birth rates and per capita CO_2 emissions were correlated with the number of threatened mammal species, their influence was indirect, through GNP.

Our path analysis also identified per capita GNP and extent of park area as having direct influences on mammalian population density (Fig. 8). Of the two, GNP has the stronger effect. Models excluding these direct links were not consistent with the data. The relationships among the socioeconomic variables included in this analysis were quite complex, and variants of the model shown in Figure 8 were also consistent with the data.

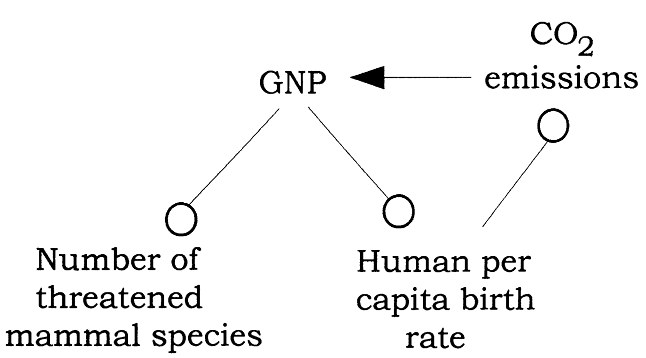

Figure 7. Path analysis diagram of the factors influencing the numbers of threatened mammal species per country (square-root transformed). Symbols are defined in Fig. 6.

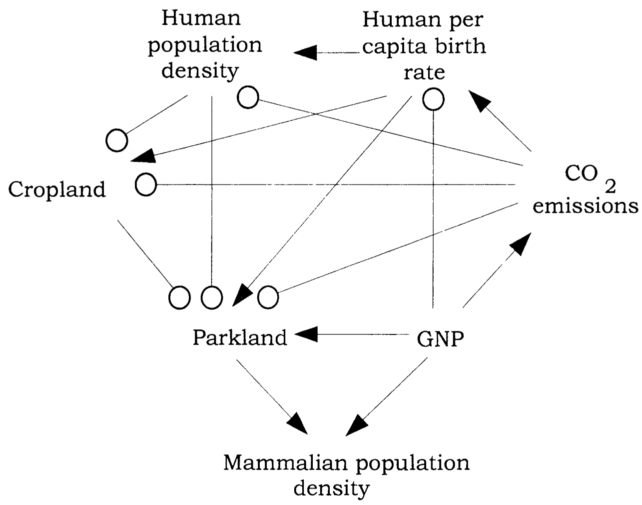

Figure 8. Path analysis diagram of the factors influencing mammalian population density (log transformed). The symbols are defined in Fig. 6.

Note that the observations of mammalian population densities came from only nine different countries. The paths between socioeconomic variables and mammalian population density are therefore based on 78 independent observations, whereas the paths among socioeconomic variables are based on only 9, each repeated several times. Therefore, although the interactions among the socioeconomic variables in the top half of Figure 8 are consistent with our particular data set, we do not believe that they necessarily represent the relationships in other countries.

Discussion

Our analysis reveals significant relationships between several socioeconomic variables and extinction risk in birds and mammals, as measured by population densities and by numbers of threatened bird species per country. The anthropogenic factors account for 28 to 50% of the variation in our measures of susceptibility to extinction. Without proving causation, these results are consistent with the hypothesis that socioeconomic conditions are related to environmental degradation and consequent species extinctions.

It seems unlikely that these socioeconomic variables are the proximate influences on species extinction. Rather, species survival is probably most often endangered by specific human activities such as habitat modification, hunting, and so forth. The particular human activities that endanger species' survival surely depend strongly upon local conditions. Nonetheless, our models based on generalized socioeconomic variables statistically explain much of the variance in the frequencies of threatened species. This suggests that similar classes of socioeconomic factors worldwide underlie the specific human activities that threaten species' survival.

The numbers of threatened bird species per country are most directly influenced by human population density and by the human birth rate, after diversity gradients and area effects are adjusted for. Note that the proportion of threatened bird species is negatively related to birth rate. Low human birth rates are associated with wealthy, developed countries (Murdoch 1983). In other words, on average, birds are most often threatened in densely populated, economically developed countries (see Table 5).

The most obvious interpretation of the correlation between human population density and the proportion of threatened bird species is habitat loss. Wright (1990) suggested that human appropriation of an increasing fraction of the Earth's primary productivity can account for observed species extinctions. Presumably this appropriation is most pronounced in densely populated countries. Yet this explanation is not entirely consistent with our results. Wright (1990) notes that over half of human appropriation of the energy fixed by ecosystems has been through agricultural lands. In contrast, our path analyses suggest that an increased proportion of agricultural land is not directly responsible for a high proportion of endangered bird species. Rather, the proportion of threatened bird species is more directly influenced by human population density or by a factor that is closely related to it. Moreover, anthropogenic effects are most pronounced in developed countries. This suggests that, contrary to numerous suggestions in the literature (Wilson 1992; Erhlich 1994), habitat loss per se does not appear to be the prime factor leading to extinction, at least for birds on the global scale. Rather, something to do with the way in which humans use habitat must be responsible.

Per capita CO_2 emissions influence numbers of threatened bird species only indirectly, through birth rates. Because of their indirect relationship to numbers of threatened bird species per country, however, it is unlikely that variables related to CO_2 emissions, such as the production of pollutants, play as significant a role in increasing extinction risk in birds, at least at the large scale examined here.

In contrast to the situation for birds, the frequency of endangered mammal species is most directly related to GNP. In other words, mammalian biodiversity loss on the global scale is related to poverty (Ehrlich & Wilson 1991). Because of the linkage between per capita GNP and subsistence hunting, and because overhunting is a major cause of the decline of mammal populations in particular, one potential reason for higher numbers of threatened mammals in poorer countries may well be increased reliance on hunting for food. Redford (1992), for example, discusses hunting pressure on neotropical rainforest fauna and concludes that mammals suffer much heavier losses in terms of individuals taken per year than do birds. It is also possible that mammals in poorer countries tend to be at greater risk of extinction because of lack of funds for conservation and enforcement agencies, such as those responsible for the control of sport hunting and poaching. These activities may also represent a major drain on mammal populations (Redford 1992). Our results are not consistent with recent hypotheses stating that poverty can lead to more-judicious use of resources and increased conservation effort (Shaw 1989). Further study is required to determine the precise mechanism through which low per capita GNP correlates with increased extinction risk among mammals. Once again, our results do not support the contention that habitat loss per se is the factor most closely related to species extinction.

Other influences of the proportion of threatened mammal species per country are apparently indirect. Per capita CO_2 emissions are correlated with extinction risk among mammals only indirectly through per capita GNP. Per capita birth rates are also only indirectly related to threatened mammal species, mostly because of their strong relationship with per capita GNP. The extent of cropland and human population per country, however, were entirely unrelated to this index of extinction risk in mammals, suggesting that mammals, to a greater extent than birds, are able to coexist with humans in agricultural or densely populated areas, at least under favorable economic conditions.

One of our most striking results is that, when nonanthropogenic influences are held constant, there is no relationship between the proportions of threatened bird and mammal species per country. As discussed above, this result suggests that different anthropogenic factors are related to elevated extinction risk among birds and mammals. Our analysis suggests that birds suffer more from factors related to demographic pressures like birth rates and human population density per country. In contrast, the proportion of threatened mammal species per country covaries with economic conditions to a greater extent than with demographic status.

Like the proportion of threatened mammal species, mammalian population density is also most directly influenced by per capita GNP. Wealthier countries tend to have higher mammalian population densities, possibly reflecting reduced levels of subsistence hunting, and/or better funding for conservation and enforcement agencies.

Mammalian population densities are also generally higher in countries with relatively extensive reserve systems. This suggests that reserves can benefit mammalian populations by maintaining their densities at higher levels than in unprotected areas. Because we controlled for total land area per country, this variable often represents the proportion of wilderness area remaining in the country. This result seems to argue in favor of reserves as conservation tools. Our results, however, do not allow us to dispel recent misgivings about their usefulness (Harris 1984; Hansen et al. 1991) because the extent of protected land per country was unrelated to the proportions of threatened bird or mammal species per country. It is possible that the high mammalian population density in countries with large extents of reserve area is a sampling artefact. In countries that have reserves ecologists may tend to preferentially sample study populations inside the reserves rather than outside. If mammal populations are higher in parks than outside, then our analysis would lead to the conclusion that countries with a high proportion of parks have denser mammal populations.

Although per capita GNP is strongly related to both the proportions of threatened mammal species and to mammalian population densities, other measures of human activity related differently to these indices of extinction risk in mammals. This difference may be a function of scale: population density is measured on local scales, while threatened status reflects a phenomenon on a national scale. Human population density, for example, may not generally reduce many mammal populations to threatened levels, but it may reduce their densities significantly.

The results we present in this study could be biased if sampling intensity were significantly different between developed and developing nations—for example if there were substantial differences in monitoring efforts for threatened species. This appears unlikely for well-studied groups such as birds and mammals. The status of birds and mammals are reasonably well known internationally (World Conservation Monitoring Centre 1992). Moreover, if there were a lower sampling effort in less-developed nations, one would expect that fewer species would be identified as threatened in poorer nations. This would lead to an inverse relationship between GNP and the proportion of threatened species. We observed the opposite, at least in the case of birds. If there is bias in the sampling, therefore, our results would likely become more significant, not less.

Several authors have proposed solutions to alleviate the loss of biological diversity, such as integration of agricultural and conservation areas (McIntyre et al. 1992), innovative taxation schemes to raise funds for conservation (McNeely 1989), and restoration of degraded areas to increase available wildlife habitat (Cairns 1988). The efficacy of these solutions will depend on the extent to which they deal with the ultimate causes of species extinction. We conclude, for example, that the integration of agricultural area and park land would probably not reduce species extinction rates, at least at a large scale, because we have found only weak or equivocal relationships between these two variables and indices of susceptibility to extinction in birds and mammals. Our results show that human population density and per capita GNP are consistently the most proximal variables to our indices of extinction risk. Reduction of pressures on natural populations stemming from these two socioeconomic conditions will be more likely to lead to the successful conservation of global species diversity.

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