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Predicting future threats to biodiversity from habitat selection by humans

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ABSTRACT

Global biodiversity is threatened by the human use, alteration and destruction of habitat. The distribution of humans among habitats should, as in other animals, be governed by density-dependent feedback on fitness. It should be possible, therefore, to merge human habitat selection – and, perhaps, other adaptive behaviours – with projections of human population size to forecast future threats to biodiversity. We evaluate this deceptively simple postulate by developing a model of human habitat selection. We test it with World Resources Institute (WRI) data and use the resulting pattern to predict threats to biodiversity. Humans select urban over rural habitats in a way that is consistent with an evolutionarily stable strategy of habitat selection. The choice of habitat is modified by per capita energy use. The pattern of habitat use is associated with increased threats to the biodiversity of mammals, birds and higher plants, but not that of reptiles. We use WRI projections of future human populations to predict the anticipated pattern of human habitat use in 2020. We then use the new distribution to calculate changes in threats to biodiversity and rank nations according to their projected threats. African nations rank consistently higher than nations from any other region. Preventive global conservation might, therefore, be most productively concentrated on helping Africa.

Keywords: Africa, biodiversity, birds, conservation, energy, isodar, habitat selection, mammals, urbanization.

INTRODUCTION

Earth is in the midst of a biodiversity crisis. Accelerated rates of species extinction foretell a major reorganization of life on our planet (Smith *et al.*, 1993; Lawton and May, 1995; Morris, 1995; Morris and Heidinga, 1997; Myers and Knoll, 2001; Woodruff, 2001). Burgeoning human populations force the hand of conservation ecologists, who must prioritize attempts to preserve biodiversity on local, regional and international scales. Currently, conservation strategies are often based on the identification of species at risk, biodiversity hotspots and areas or ecosystems under extreme threat (e.g. Hunter, 1996; Meffe and Carroll, 1997; Myers *et al.*, 2000). But there are increasing calls for coordinated

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efforts to set objective priorities for conservation (da Fonseca *et al.*, 2000; Mace *et al.*, 2000). In each case, conservation efforts would be enhanced greatly by the development of indicators that could predict threats to biodiversity.

Models in evolutionary ecology suggest a very powerful approach based on the optimization research program (Mitchell and Valone, 1990; Rosenzweig and Abramsky, 1997; Rosenzweig, 2001). Organisms responding to environmental challenges should possess adaptive behaviours. Ecologists ought to be able to map these adaptations onto underlying gradients associated with threats to biodiversity; for example, changes in habitat that alter predatory risks and other foraging costs can, with appropriate experiments, be detected in the behaviour of optimal foragers (Brown, 1988, 1992; Brown and Mitchell, 1989; Brown *et al.*, 1990). At larger scales, density-dependent habitat selectors alter their relative abundances among habitats in response to changes in competition (Rosenzweig, 1974, 1979, 1981, 1991; Abramsky *et al.*, 1991, 1994; Morris, 1988, 1989, 1999; Morris *et al.*, 2000, 2001) and predation (Rosenzweig *et al.*, 1997; Abramsky *et al.*, 1998).

We propose, and illustrate, a variant of the adaptive approach by mapping the global habitat selection of humans against current and projected threats to biodiversity. Rather than despair at the inertia of human population growth and migration, we use it to forecast which nations are likely, over the next two decades, to face the greatest increase in threats to their biodiversity.

We begin with an overview of theories of habitat selection as they can be applied to humans occupying urban versus rural habitats. We use World Resources Institute (WRI) data on human population sizes in 1980 to test whether humans select habitat in agreement with the theory's predictions. They do. We validate the model with population estimates for 2000, merge the global pattern of human habitat use with WRI data on the number of threatened species in several taxa, and predict threats to the biodiversity of each taxon. We use WRI population projections through 2020 to re-calculate the pattern of human habitat use, then use that pattern to compute, and rank, the expected increase in risks to biodiversity for 144 nations.

A THEORY OF HUMAN HABITAT SELECTION

When faced with a choice of alternative habitats, an optimally behaving individual should occupy the habitat that maximizes its Darwinian fitness. Individuals obeying such an evolutionarily stable strategy should distribute themselves so that each individual's expected reproductive success is the same in all occupied habitats (Fretwell and Lucas, 1970; Rosenzweig, 1981; Morris, 1988). The resulting ideal distribution of individuals can be revealed by plotting the densities of individuals in adjoining pairs of habitats (the habitat isodar; Morris, 1987, 1988, 1989, 1999). Such habitat isodars have been drawn successfully for a variety of species, including rodents (Morris, 1988, 1992, 1994, 1996; Abramsky *et al.*, 1991, 1997; Knight and Morris, 1996; Morris *et al.*, 2000, 2001), salmonid fishes (Rodríguez, 1995; Knight, 2000) and birds (Fernandez-Juricic, 2001). The theory, and its empirical tests, lead us to three intriguing questions: Are humans density-dependent habitat selectors? If they are, can their habitat-selection strategy be detected with isodars? Can isodars forecasting future patterns of human distribution also be used as leading indicators of threatened biodiversity?

Our point of departure is the generalized logistic equation (Gilpin and Ayala, 1973) in two different habitats

$$\frac{1}{N_1}\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1\left(1 - \left(\frac{N_1}{K_1}\right)^{\theta_1}\right) \tag{1}$$

and

$$\frac{1}{N_2}\frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2\left(1 - \left(\frac{N_2}{K_2}\right)^{\theta_2}\right) \tag{2}$$

where r_i is the intrinsic rate of population growth in habitat i, N is density, K represents carrying capacity and θ is a coefficient of curvature that represents the amount of interference among competitors. If individuals select habitats in a way that maximizes fitness, and if individuals are free to occupy the habitats that they choose, the densities in the two habitats should be adjusted such that the expected fitness of an individual is the same in both (Fretwell and Lucas, 1970), thus

$$\frac{1}{N_2}\frac{\mathrm{d}N_2}{\mathrm{d}t} = \frac{1}{N_1}\frac{\mathrm{d}N_1}{\mathrm{d}t} \tag{3}$$

Following substitution from equations (1) and (2),

$$r_2 - \left(\frac{r_2 N_2}{K_2}\right)^{\theta_2} = r_1 - \left(\frac{r_1 N_1}{K_1}\right)^{\theta_1} \tag{4}$$

Before we can apply equation (4) to humans, we need to identify relevant habitats between which people can choose. Relying on the wisdom of demographers, we selected rural versus urban environments as appropriate habitat choices. Neither we, nor the theory, assume that humans are perfectly adapted to either habitat. We do assume that humans can distinguish between rural versus urban habitats, and have the ability to choose one habitat over the other, but not necessarily that their choice is adaptive. Thus, the behaviour of habitat selection is an adaptation, but its expression for any pair of habitats is subject to evolutionary, historical, behavioural and ecological constraints.

We also assume that, within individual nations, humans can exercise their choice as to which of the two habitats they wish to live in (this does not exclude the possibility that dominant or resident individuals, or associated social values and government policies, might influence habitat choice). In the context of equation (4), and at the scale of entire nations, r represents a variable reflecting individual success at different densities and N corresponds to the population living in each habitat. As density declines toward zero, urban environments become ever more 'rural' and both habitats necessarily converge on the same maximum per capita fitness values ($r_2 = r_1$). Bearing these points in mind, we simplify equation (4) to the linear isodar (Morris, 1988, 1994),

$$\log N_U = \left(\log K_U - \frac{\theta_R}{\theta_U}\log K_R\right) + \frac{\theta_R}{\theta_U}\log N_R \tag{5}$$

where $U = 2$ and $R = 1$ and represent the set of urban (U) and rural (R) population sizes where the expected fitness of an individual is the same in both. When organisms select habitat in a way that maximizes their individual fitness, the isodar represents the solution to the evolutionarily stable strategy of habitat selection (Morris *et al.*, 2001).

Important insights into patterns of human population regulation can be gleaned from the isodar. Differences in the amount of interference between rural and urban habitats, for example, will be revealed if the slope of equation (5) departs from unity. Equation (5) also yields the expected pattern of carrying capacities in the two habitats. To see this latter point, note that the general isodar equation can be written as

$$\log N_U = A + b(\log N_R) \tag{6}$$

where A is the isodar's intercept and b is its slope (both of which are known). From equation (5), we see that

$$b = \frac{\theta_R}{\theta_U}$$

and

$$A = \log K_U - b(\log K_R) \tag{7}$$

Thus

$$\log K_U = A + b(\log K_R)$$

and the isodar gives a perfect 'match' between population size and carrying capacity (Parker, 1978; Pulliam and Caraco, 1984; Fagen, 1987; Morris, 1994).

METHODS

Human habitat selection

We obtained human population data from tables published by the World Resources Institute (WRI, 1998) that include United Nations Population Division (1996 Revision) estimates of overall population size, and the proportion of urban residents, for 157 nations. We used the data for 1980 to build our main model of urbanization, then validated it with WRI (UN) projections of urban populations in 2000. We excluded three nations [Singapore, which has no rural population, as well as China and India, whose total populations exceed the next most populous nation (USA) by a factor of three]. We used linear regression (SPSS, 1999) on the logarithmically transformed densities to test for significance of the human isodar, then used geometric-mean regression (Sokal and Rohlf, 1981) to generate the final isodar model.

The resulting human isodar appeared heterogeneous. We attempted to account for the heterogeneity by using the WRI data tables to create a series of binary variables representing low (equal to or below the median) and high (above the median) values for a variety of measures that could represent the perception of urban versus rural habitat quality by individual humans (Table 1). We chose a binary scale because the distributions of many of the variables cannot be transformed easily to meet the assumptions of parametric analyses (those distributions were often also bimodal), and because the preliminary isodar bifurcated into two predominant classes of nations. Some variables (e.g. per capita CO_2 emissions, percent of land in domestic use) were available only for the period around 1995. We selected values for all other variables from the same time frame. We recognize that these data are more recent than our data on urban versus rural habitat use, and thus cannot reflect actual values used by humans in assessing habitat in 1980. In all cases, however, it is reasonable to assume very high correlations between the values of the variables we use here (particularly

Table 1. List of World Resources Institute (WRI) variables used in the isodar analysis: all variables except 'Rural' were converted to a binary scale to represent the quality of urban versus rural habitats

Variable	Description
Carbon*	Per capita carbon dioxide emissions in 1995 (metric tonnes)
Domland*	Percent of total land area in domestic use (1994)
Forcent*	Percent closed forests in 1996 compared to original forest cover
Forchange*	Percent annual mean change in forest cover (1990–95)
Forcover*	Total area covered by closed forests (1996, 1000's of ha)
GDP*	Per capita GDP in $US (1995; exchange rate based)
ODA*	Per capita official development assistance in $US (1995)
Popchange*	Percent mean annual population change (1995–2000)
Popden*	Human population density (1996, 1000 ha^{-1})
Rural	Log_{10} rural population size (thousands)

Note: Asterisks indicate variables also used in exploratory analyses that assessed possible relationships of economic and demographic indicators with threatened biodiversity (Table 2). Descriptions and assumptions of all variables can be found in the appropriate WRI (1998) data tables.

because they are measured on a binary scale) and their values in somewhat earlier time frames. Our use of values for the period around 1995 is also appropriate because we validate our model with projections of rural and urban densities in the year 2000 (see Results).

We re-analysed the isodar with multiple regression by forcing rural population size into the model, and only then did we include the binary variables in stepwise fashion (SPSS, 1999) until no additional variable could improve the fit of the equation (regression coefficient not different from zero; $P = 0.05$). Sample sizes for the independent binary variables were less than for human population size (data not available for all nations). We examined the proportion of variation explained at each step in the multiple regression to search for large differences in the amount of explained variation that would justify using a simpler model.

The isodar represents our best available solution to global habitat selection by humans. We define each nation's 'isodar score' as the urban density predicted for it by the final multiple regression equation of the isodar. The equation was constrained to include the logarithm of rural density plus any statistically and biologically significant fixed binary variables.

Predicting the threat to biodiversity

We used the WRI biodiversity tables to calculate the percent of mammals, birds, higher plants and reptile species known to be under threat according to IUCN criteria I–IV (WRI, 1998; most biodiversity data reflect values for the period between 1994 to 1996 and correspond with the time period used for the binary variables representing habitat quality). Again, the data could not be easily transformed to meet the requirements of parametric statistical methods, so we created categorical variables for each taxon that corresponded to whether the percent threat was below, or equal to or above, the median value for all nations in the sample. The binary variables reflect, for each taxon, whether the threat to that taxon's biodiversity is high or low. We checked for major discrepancies with more recent tables on biodiversity (WRI, 2001) in an attempt to ensure that our binary estimates were as current as possible. We did not use the 2000 tables exclusively because time periods for some variables, including the human population estimates, were not updated from 1998, whereas others, representing 'habitat quality', had been. Use of the 2000 tables would thus increase the time interval between human population size and our binary estimates of habitat quality.

We tested whether the threat to biodiversity for each taxon could be predicted from the human isodar by using the binary logistic regression equation

$$Q = \frac{e^{B_0 + B_I X_I}}{1 + e^{B_0 + B_I X_I}}$$

(Q is the probability that a country belongs to the high-threat group of nations, B_I is the logistic regression coefficient, and X_I is the value of the isodar) to calculate the probability (Q) that a nation belonged to the high-threat group (Norušis, 1999). The analysis includes a 15-year lag between the population (1980) and biodiversity estimates (~1995). We do not know what the most appropriate time lag might be, but we are certain that there is no instantaneous response of IUCN biodiversity assessments to changes in human habitat use.

We used WRI (1998) population projections to calculate the expected urban and rural population sizes for all nations in 2020, and calculated the expected values of the human isodar based on the 1980 multiple regression solution. We then used the solutions to the logistic regression equations to calculate the new probability, again for each nation, that it belonged to the high-threat group. We calculated the summed difference across taxa, between the original probability of a nation belonging to the high-threat group, and that based on the population projections in 2020. The summed difference identifies those nations for which the predicted increase in threat to biodiveristy is greatest; those nations deserve urgent and preventive attention for the conservation of their biodiversity.

Processes influencing isodars

An increased threat to biodiversity, in our analysis, is always correlated with an increase in the isodar score that is influenced by two processes: population increase and increased urbanization. Population increase, *ceteris paribus*, will always act to increase the predicted value of the isodar, but its effect can be weakened by increased urbanization (reduces the magnitude of population size in the rural habitat used to calculate the isodar). We assessed the relative effects of these processes on the 2020 isodar with stepwise linear regression against two independent variables: (1) the ratio of total population size in 2020 relative to 1980 (a measure of 'population growth') and (2) the proportional increase of the rural population (relative to 1980) divided by the proportional increase in the total population (a measure of 'rural stability'; a value of unity would represent a nation where the proportion of the population living in the rural habitat remained constant; a value more than one means that the rural component is an increasing proportion of the total population).

Other economic and demographic indicators of threatened biodiversity

We were concerned that significant isodars might reflect little more than the influence of human population density, population size and population growth on threats to biodiversity. We included these and 20 other measures in a parallel exploratory binary logistic regression analysis evaluating possible economic and demographic predictors of threats to biodiversity (Table 2). We identified candidate variables by searching the WRI database of 157 nations for a variety of national statistics that might act as indicators of threats to biodiversity. To pass our initial screening (aimed at maintaining large and representative sample sizes), estimates of each variable had to exist in at least 140 different nations. We selected variables with the largest sample sizes that represented economic, population, agriculture, freshwater, forests, land cover, energy and atmospheric indicators. We included the density of species per 10,000 km^2 as an additional variable to allow a comparison among nations with vastly different levels of biodiversity. The WRI estimate is based on a species–area curve ($S = CA^z$) and calculates the expected density of species that would occur in a standard area of 10,000 km^2. The slope of the species–area curve was estimated by the WRI as $z = 0.33$. The estimate is thus a rather crude indicator of species density because z is known to differ among biological provinces and climates (Rosenzweig, 1995). Nevertheless, it is advocated as a useful indicator (National Research Council, 2000). We compensated for errors in the estimates of species density by converting the variable to a binary scale (below). Details on the quality and sources of all data are outlined in the respective WRI tables (WRI, 1998).

As above, many variables could not be easily transformed to meet the assumptions of parametric analyses, whereas others (e.g. species density) were too crude to use as interval-scale measures. We solved both problems by splitting each variable at its median value. Nations with values equal to, or less than, the median were placed in

Table 2. List of World Resource Institute (WRI) variables converted to a binary scale and evaluated by stepwise logistic regression as significant international indicators of threats to biodiversity

Variable	Description
Agprod	Percent agricultural production for 1994–96 relative to 1989–91
CO_2	Total carbon dioxide emissions in 1995 (1000's of metric tons)
Energyprod	Total commercial energy production in 1995 (petajoules)
Fert	Annual fertilizer use in 1994 ($\text{kg} \cdot \text{ha}^{-1}$)
Numprot	Number of protected areas (IUCN categories I–V)
Popsize	Human population size in 1998
Protarea	Protected area (% of total area in IUCN categories I–V)
Spden	Species density by taxon (number × 10,000 km^{-1})
Totcrop	Total cropland in 1994 (1000's of ha)
Totforest	Total forest area in 1995 (1000's of ha)
TotGDP	Total GDP in $US millions (1995; exchange rate based)
Totland	Total land area (1000's of ha)
TotODA	Mean annual official development assistance 1993–95 ($US millions)
Wateruse	Annual withdrawal of freshwater (% of that available)

Note: Additional variables included in the analyses are listed in Table 1 (denoted by asterisks). Descriptions and assumptions of all variables can be found in the appropriate WRI (1998) data tables.

the ‘low’ category; nations with values exceeding the median were placed in the ‘high’ category. We used forward stepwise logistic binary regression based on the likelihood-ratio test for variable removal, with all independent variables coded as 0 and 1 (Norušis, 1999). We assessed each model on the significance of the overall χ^2 and on the Nagelkerke R^2. Our objective was to develop a general explanatory model highlighting indicators that increase or reduce threats to biodiversity, rather than finding the best predictive model possible.

RESULTS

The human isodar

The human isodar was highly significant and explained over 50% of the variation in urban population size (Fig. 1a). The 95% confidence interval for the slope was greater than 1 (1.01–1.26). Thus, on a global scale in 1980, the isodar reveals a significant coefficient of curvature: as the population grows, an increasing proportion of people live in urban habitats. Similarly, the corresponding confidence interval for the intercept was less than zero (– 1.05 to – 0.15): irrespective of the change in the proportion of people living in urban areas, rural population size in nations with relatively small human populations exceeded that of urban areas.

Careful inspection of the 1980 isodar suggests that it may be heterogeneous, a conclusion made more apparent by examining the isodar on a linear scale (Fig. 1b). The isodar bifurcates into two more-or-less equal classes of nations, those with relatively high urban population sizes and those with relatively high rural populations.

We tried to explain the isodar’s heterogeneity with a second analysis that included variables representing habitat quality (Table 1). Four of these additional variables helped to explain over 80% of the variation in urban population size (Table 3; $F_{5,133} = 121.2$; $P < 0.001$). Urbanization was greater in nations with a high per capita gross domestic product (GDP) and with low forest cover, and was less in nations with high rates of popula-

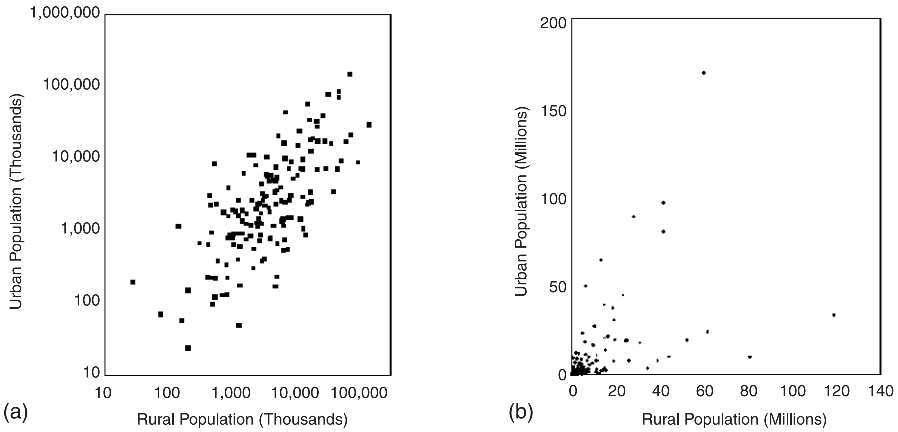

Fig. 1. The relationship between urban population size and rural population size in 1980 (isodar) for 154 nations. (a) logarithmic scale; (b) linear scale.

Table 3. Significant variables accounting for urban population size

Step	Variable	b	t	P	R^2_{adj}
	Constant	0.39	2.1	0.039	
1	Rural	0.78	15.8	0.000	0.51
2	Carbon*	0.38	4.5	0.000	0.76
3	GDP*	0.27	3.2	0.002	0.79
4	Popchange*	−0.28	−4.1	0.000	0.80
5	Forcover*	0.2	3.1	0.002	0.81

* Scored 0 (low) and 1 (high).

tion growth. But by far the most significant variable, and the one accounting for far more variability in urbanization than any other, was the per capita carbon dioxide emissions in 1995 ($\simeq$ energy consumption). Consequently, we grouped nations into low and high categories corresponding to their binary values of per capita CO_2 emissions [$\log N_U = 0.72 + 0.86\ (\log N_R) - 0.7(CO_2)$; $F_{2,146} = 220.6$, $P < 0.001$; $R^2_{\mathrm{adj}} = 0.76$], and obtained near-perfect separation along the isodar (Fig. 2; $P \leq 0.001$ for 'both' isodars, the particular negative coefficient associated with energy consumption is specific to our binary coding in this analysis). The 76 nations with low CO_2 emissions had relatively higher rural than urban population sizes (the 95% confidence interval about the y-intercept falls beneath 0), whereas population densities in the two habitats were similar in the 73 nations with high CO_2 emissions (95% confidence interval = – 0.19 to 0.66). Neither slope was different from unity. Thus, the apparent curvature in the global analysis, which causes the proportion of humans living in urban environments to increase with population size, is intricately intertwined with the extent of urbanization. Urbanization, in turn, is correlated with per capita energy use.

We validated the model by applying the same classification to the population estimates in 2000. Differential urban migration in low-energy nations would tend to destroy the binary separation of the two isodars. Again, both isodars were highly significant (Fig. 2; $P < 0.001$). Neither slope was different from unity, the population size (and expected carrying capacities, equation 7) was similar in the two habitats in low-energy nations (95% confidence interval about the intercept = – 0.62 to 0.34), but urban population size was greater than rural population size in high-energy nations (the 95% confidence interval about the y-intercept lies above 0). Through time, all nations became more urban, but the extent of urbanization was linked tightly to per capita CO_2 emissions.

The threat to biodiversity

Three of the four binary logistic regressions successfully predicted whether threats to biodiversity were high or low (Table 4, Fig. 3). The probability of a nation having higher than average (median) threats to mammal, avian and plant biodiversity increased with the nation's isodar score (Fig. 3). There was no relationship between the threat to reptilian diversity and the human isodar [this may be related to the low diversity of reptiles in our sample relative to the other vertebrate groups (median richness for reptiles, mammals and birds = 70, 128 and 295 species respectively)].

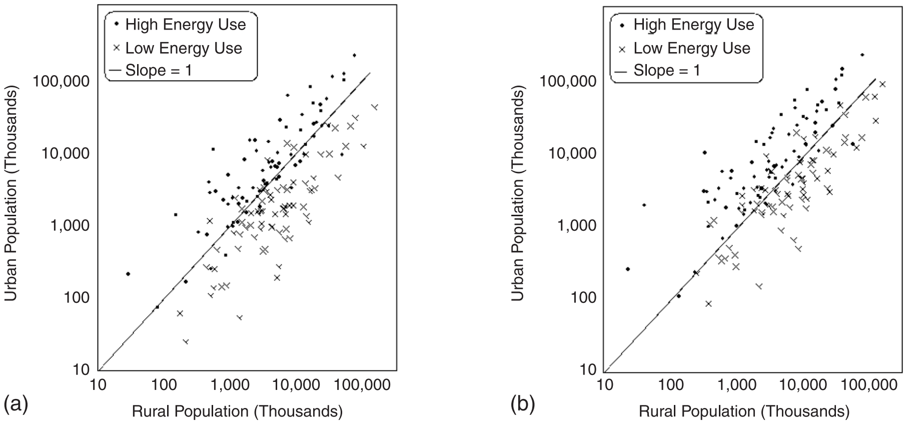

Fig. 2. The relationship between urban population size and rural population size (isodar) for 149 nations classified as being either above or below the median per capita CO_2 emissions in 1995. (a) data for 1980; (b) data projected for 2000. The reference line has a slope of 1.

If values of urban population size predicted from isodars indicate threats to biodiversity, might not actual values be even better indicators? We tested this postulate with a second set of stepwise binary logistic regressions on threats to biodiversity of the four taxa that included, for each nation, its 1980 isodar score, the log-transformed actual urban population size, the proportion of humans living in urban environments (square-root arcsin transform) and the binary measure of per capita CO_2 emissions. In each of the three significant regressions (mammals, birds and plants), only isodar values were retained in the final forward-stepping model (log-transformed urban population size was a significant predictor of threat but was inferior to, and redundant with, the isodar). To make our analysis as robust as possible, we repeated it using backward elimination and obtained identical outcomes for both birds and plants. Urban population size and the proportion of humans occupying urban environments were retained in the analysis for mammals, but the

Table 4. Human occupation of urban versus rural habitats successfully predicted threats to biodiversity for three of four taxa (logistic regression)

Taxon	Source	*B*	*WALD*	d.f.	*P*
Mammals	Isodar	1.31	15.6	1	< 0.001
	Constant	−4.45	15.2	1	< 0.001
Birds	Iosdar	1.22	14.6	1	< 0.001
	Constant	−4.23	14.4	1	< 0.001
Plants*	Isodar	0.86	7.7	1	0.005
	Constant	−2.91	7.5	1	0.006
Reptiles					N.S.

*Higher plants only.

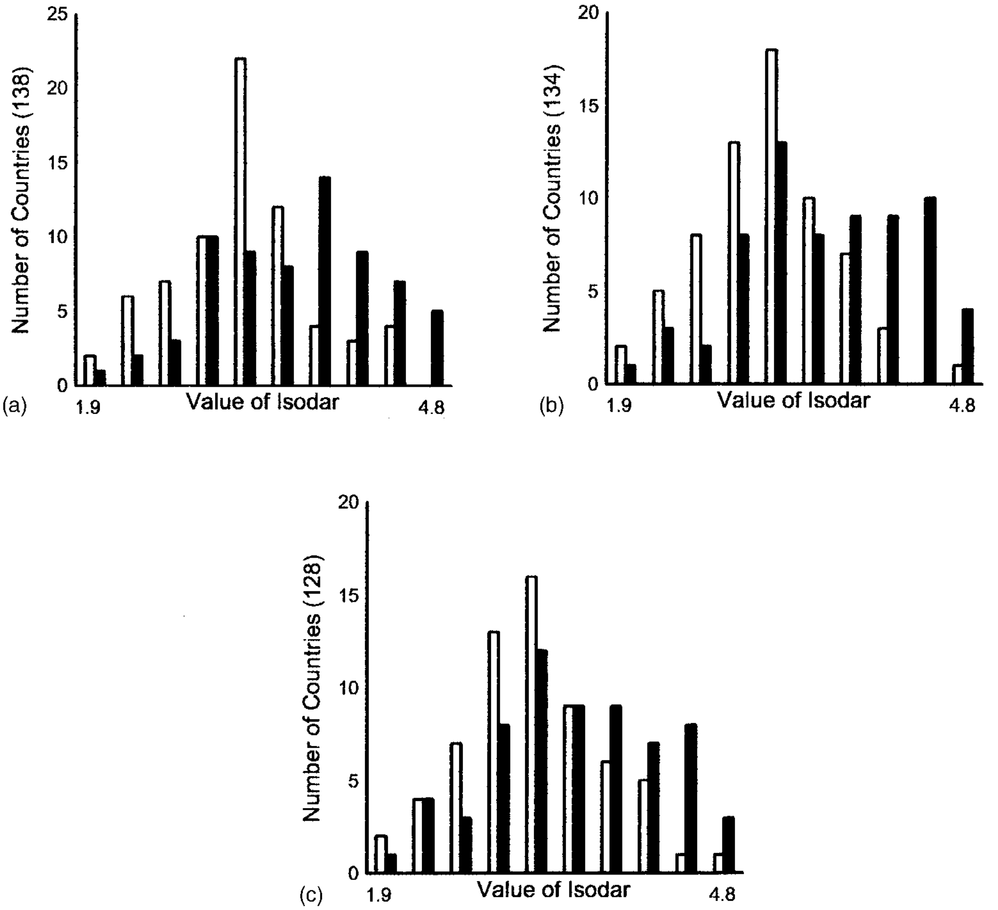

Fig. 3. The relationship between global threats of extinction and the human isodar. Nations whose human isodar has a high value have a greater proportion of their (a) avian, (b) mammal and (c) plant biodiversity under threat of extinction than do nations with a lower isodar value. ■, a high proportion of species under threat of extinction; □, a low proportion of species under threat of extinction.

model explained less variation than did the simple univariate regression using only the human isodar (Nagelkerke $R^2 = 0.159$ for the backward solution *vs* 0.174 for the isodar alone). No variable was a significant indicator of threats to reptilian diversity using either procedure.

The 2020 isodar was highly correlated with that from 1980 and, although all nations tended to have higher isodar scores, the relative increase was greatest in nations with correspondingly low rates of urbanization in 1980 [2020 isodar = 0.31 + 0.93 (1980 isodar); $F_{1,147} = 1357.3$, $P < 0.001$; Fig. 4]. The probability of a nation's threat to biodiversity being above the median for all nations increased accordingly (repeated-measures analysis of variance; $F_{1,133} = 19.4$, $P < 0.001$; $F_{1,137} = 14.2$, $P < 0.001$; $F_{1,127} = 17.5$, $P < 0.001$ for mammals, birds and higher plants, respectively). Most importantly, there was no evidence that any nation's 2020 isodar was anomalous with that calculated for 1980.

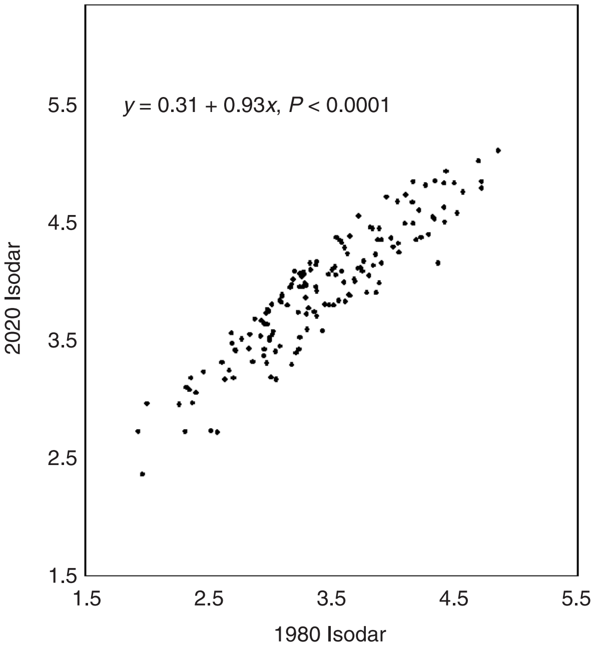

Fig. 4. The expected values for the human 2020 isodar were highly correlated with those calculated from the 1980 isodar.

Predicted increases are greatest in Africa

We were able to calculate valid isodars and associated threats to mammal, avian and plant biodiversity in 118 of the 157 nations in the WRI inventory. The summed differences of the probabilities of belonging to the group of nations with 'high' threats to biodiversity increased in 80 nations. Nineteen of the 25 nations with the greatest increase in threats to biodiversity are located in Africa (Appendix 1). All of the 44 African nations were ranked in the 77 nations with the greatest cumulative threats to biodiversity. No African nation is included in the 38 (primarily European) countries where the summed differences in probable threats to biodiversity declined.

Simply counting the number of nations with high future threats to biodiversity might mislead conservation efforts if those nations tend to be of small size, or if they harbour low diversity. We evaluated these possibilities with respect to Africa by testing for significant differences among the 19 highest-ranked African nations, the other 25 African states and the 74 remaining states listed in Appendix 1. There is no significant difference in area among the different classes of nations (Kruskal-Wallis non-parametric analysis of variance; $H_2 = 4.39$, $P = 0.11$; Fig. 5). African nations possess more species of mammals and birds than do the remaining states ($H_2 = 10.63$, $P = 0.005$ and $H_2 = 7.6$, $P = 0.02$ for mammals and birds, respectively; there was no difference between the two classes of African states: $H_1 = 1.64$, $P = 0.2$ for mammals, $H_1 = 2.34$, $P = 0.13$ for birds), but not more species of plants ($H_2 = 2.67$, $P = 0.26$; Fig. 6). The 'African pattern' is not caused by small area or reduced diversity.

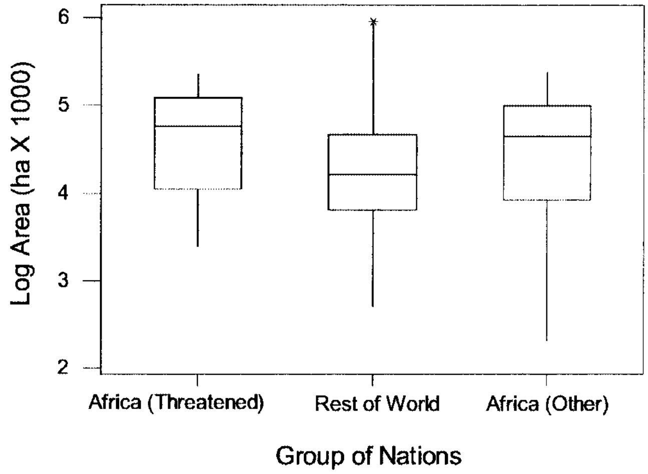

Fig. 5. Box-and-whisker plots illustrate no significant differences in the area of the 19 African nations with high future threats to their biodiversity and that of the 25 remaining African nations, or of the 74 other nations listed in Appendix 1 (asterisk < three times the inter-quartile range).

The African pattern permeates the entire data set. There is no rank correlation between the cumulative threat to biodiversity and area (Kendall's $\tau = 0.09$; $P = 0.16$, $N = 118$) or plant diversity [$\tau = 0.11$; $P = 0.09$, $N = 117$ (total plant diversity in the United Arab Emirates is unknown, but no species is listed as threatened)], but there is a significant rank correlation with both the number of mammal ($\tau = 0.3$; $P < 0.001$, $N = 118$) and bird ($\tau = 0.28$; $P < 0.001$, $N = 118$) species. Conservation efforts that help nations with high cumulative threats would also help nations with high vertebrate diversity.

The Republic of Korea deserves special mention. The rural population, and thus the isodar, will be less in 2020 than in 1980, giving Korea the lowest ranking of all nations for which we could calculate future threats to biodiversity. The effect occurs, despite modest growth in population size (38 million in 1980, 51.7 million in 2020), because there will be a remarkable increase in urbanization (57% in 1980, 93% in 2020), which may cause the isodar to underestimate increased threats to Korea's biodiversity.

We were able to rank an additional 26 nations for which only subsets of taxa were available to assess threats to biodiversity (Appendix 2). The only African nation in the list (Botswana) had a very low ranking caused, as in Korea, by moderate population growth (0.9 million in 1980, 2.4 million in 2020) and the largest projected shift in urbanization of all nations (15% in 1980 *vs* 89% in 2020).

Do the data warrant ranking nations by the threats to their biodiversity?

Our analyses explain relatively small amounts of the variation in threatened biodiversity and depend critically on the percentage of each taxon listed under IUCN criteria. The reliability of the data is likely to vary dramatically among nations because our knowledge of even well-known groups is heterogeneous. Nations differ in the richness of their biotas, in the number of scientists studying them, in the allocation of resources to

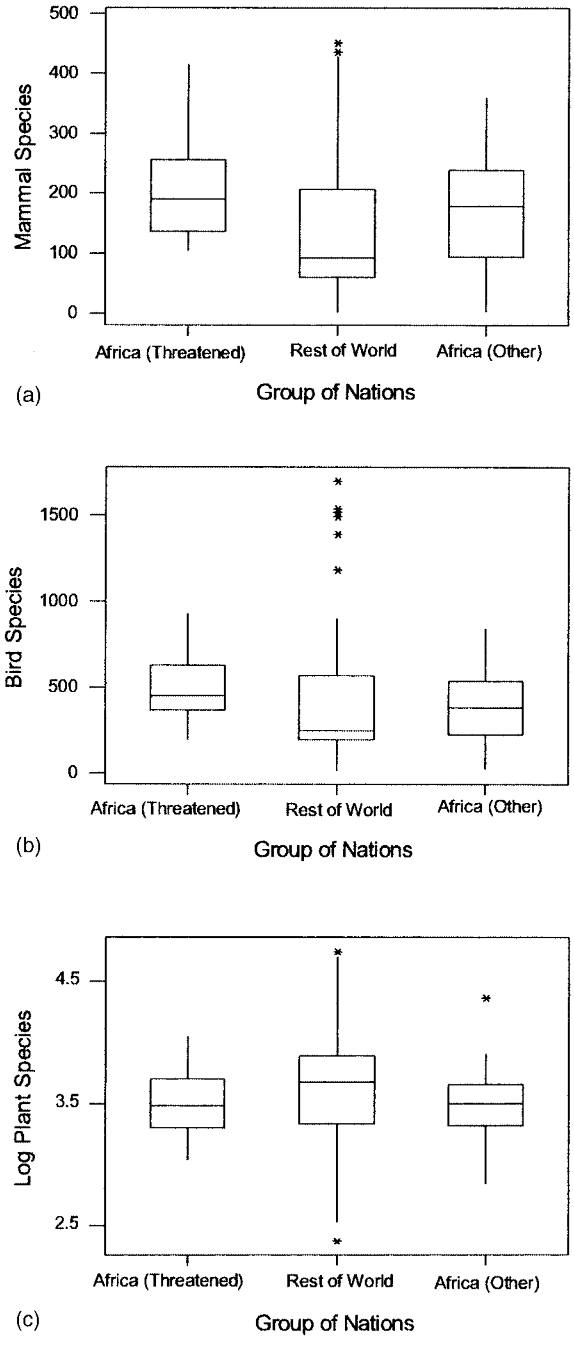

Fig. 6. Box-and-whisker plots reveal that African nations possess higher medians for the number of (a) mammal and (b) bird species than the remaining 74 nations listed in Appendix 1. (c) There is no difference in plant diversity (asterisks > three times the inter-quartile range).

biological knowledge, and in the logistical and financial capacity to study biological diversity. Such disparities may influence which nations are estimated to have relatively high and low threats to their biotas, and thus may influence the predictive equations relating those threats to human habitat selection. However, our data fail to reveal such an effect. The ranking of nations is remarkably similar whether ranked on the basis of individual taxa or on the summed increase in threats across taxa (Appendix 1).

Additional concerns could include biases in demographic projections and an emphasis on nations that currently have relatively low probabilities of 'high threats' to their biodiversity. Such concerns must not deter us from pre-emptive efforts to reduce future risks to biodiversity. Although applications of our method may be best applied using carefully constructed and geographically referenced databases, such as those used by Balmford *et al.* (2001) and Cincotta *et al.* (2000), recall the primary question of our analyses: Can we use human behaviour as a leading indicator of threats to biodiversity? The unequivocal answer is yes.

Isodars increased most in nations with high and stable proportions of rural residents

Stepwise linear regression revealed that isodars increased most in nations with both high growth in total population size and a stable proportion of rural residents ($F_{2,146} = 306.4$, $P < 0.001$, $R^2_{\text{adj}} = 0.80$; Table 5). Thus, population growth was correlated with stability in a nation's rural component of the population and there was no trend for the two processes to be traded-off one for the other.

Threats to biodiversity are correlated with other indicators

All binary logistic regression analyses assessing other possible economic and demographic indicators were highly significant (Table 6). The patterns vary among taxa. Nations with high human population density also have a high proportion of their native reptiles threatened with extinction. Wealthy nations (high GDP) have a high proportion of both mammals and birds under threat of extinction. Nations that have set aside relatively large areas for protection are also those that have a small proportion of birds and mammals threatened with extinction, but such nations may have, nevertheless, a high proportion of their flora living with extinction risk. The proportion of threatened birds is highest in nations with high agricultural production, whereas nations using a high proportion of their fresh water also have a high proportion of plants and mammals under threat. Sadly, nations

Table 5. The magnitude of population growth, and the relative stability of a nation's human population living in rural areas, contribute positively to increases in predicted isodar scores between 1980 and 2020 (stepwise linear regression; $F_{2,146} = 306.4$, $P < 0.001$)

Variable	*b*	*t*	*P*
Constant	−0.51	−11.7	< 0.001
Increase in total population	0.22	20.7	< 0.001
Rural increase relative to total	0.86	15.7	< 0.001

Table 6. Summary of stepwise binary logistic multiple regression analyses searching for significant international binary indicators of threats to the biodiversity of four global taxa

Taxon	Variables associated with increased threats	Variables associated with reduced threats	χ^2	*P*
Reptiles	Popden		8.15	0.004
Birds	TotGDP Agprod	Protarea	40.09	0.000
Mammals	Popsize TotGDP Wateruse	Protarea	38.34	0.000
Higher plants	Wateruse Spden (plants) Numprot		24.75	0.000

Note: Only significant variables are listed.

with the greatest density of plant species are also those whose floras face the highest extinction risk.

Readers beware! We report the results of the exploratory analyses because they reveal what may be useful, or otherwise instructive, patterns of association. The patterns of association may also represent little more than spurious correlations. The primary purpose of our analysis was not to assess all possible associated variables, but rather to evaluate whether relationships between isodars and threatened biodiversity reflected nothing more than correlated indicators of human density and endeavour. On this point, our results are clear. Although human population size was a significant predictor of threats to mammal diversity, no other measure of human population size and demography successfully predicted threats to mammals, or to birds and plants. The relationship between isodars and threats to biodiversity is caused by more than just the influences of human density and population size; it depends on the pattern of density-dependent habitat selection.

DISCUSSION

Adaptive human behaviour, reflected in the isodar of selection for urban versus rural habitats, appears to be a reasonable and leading indicator of threats to the world's biodiversity. As such, we believe that human habitat selection can be used to identify those nations most likely to face increased threats to their biodiversity over the next few decades. Rather than despairing about inevitable increases in human numbers, we have tried to turn the life-history inertia of our long-lived species to advantage by building on demographic projections of human population size and migration. The projections provide a rank ordering of nations most in need of preventive conservation. At the world scale, many of those efforts should be directed towards helping Africa.

It is important to keep in mind, however, that the extent of urbanization, and hence our ability to predict threats to biodiversity, is highly dependent on whether per capita energy consumption is high or low. Nations with low energy consumption lie along a lower isodar than do those with high consumption. The two isodars merge when we include energy use. Thus, by including energy in the isodar, we have effectively standardized the pattern of human habitat use between the two kinds of nations. One might wonder whether per capita energy consumption would be a valid predictor of threatened biodiversity by itself. When we tested this option, there was no significant association for mammals ($P = 0.09$), and the significant pattern for birds and higher plants ($P = 0.03$ and $P = 0.04$, respectively) paled in comparison with that of the isodar that includes energy use ($P < 0.005$ in all cases). It is thereby apparent that the interaction between energy use and habitat selection influences the overall threat to biodiversity.

It is intriguing, nevertheless, that per capita energy consumption helps to explain a substantial portion of the variance in the number of people living in urban environments. We have known, for a long time, that nations with high per capita energy consumption have high rates of urbanization. In the context of the isodar, per capita energy consumption may represent a variable that improves the 'quality' of urban habitats, one that facilitates urbanization, or one that simply emerges when humans congregate in urban environments. Exploratory analyses reveal that other variables, especially those reflecting economic activity, are also highly associated with urbanization, but are redundant with per capita energy consumption. Again, some might wonder whether energy use drives economic activity, or emerges because of it. Our purpose was not to develop the very best model for human occupation of urban habitats, but rather to develop a model of human behaviour and biodiversity that could be extended into the future. We suspect that a binary variable reflecting a nation's relative energy consumption is more likely to be stable than variables measuring its GDP.

Why bother with the isodar? Demographers have already calculated expected urban population sizes. Why not use those values directly to estimate current and future extinction risks? The answer is simple. The isodar does a better job of indicating threats to biodiversity than does the actual number of people living in urban environments. We interpret this non-intuitive result to reflect four key elements: (1) that the distribution of humans between the two habitats is at least as threatening to biodiversity as is urban population size; (2) that the distribution of humans differs between nations with high and low energy use; (3) that the interaction between energy use and human distribution modifies threats to biodiversity; and (4) that threats to biodiversity are thereby intricately interrelated with the behavioural strategy of human habitat selection.

Our use of isodars might be more convincing if we were able to test the postulate that human habitat selection tends to equalize the expectations of fitness (or their socio-economic correlates) between urban and rural residents. Such an analysis may be impossible and is beyond the scope of our current objectives. It may also be unnecessary. Even if human choices of habitat do not currently represent an evolutionarily stable strategy, it is clear that the occupation of urban versus rural habitats, and the behaviour that drives it, is remarkably consistent. We find it an astonishing fit with evolutionary theory that nations with dramatic differences in economic, political and social systems, in cultural and religious values, in history, and in racial and ethnic composition, follow similar patterns of human abundance in rural and urban habitats. Sceptics who are unconvinced that the uniform global pattern of urbanization depends on density-dependent habitat selection will need to propose a more parsimonious alternative.

It is possible, nevertheless, that part of the isodar pattern is related to the arbitrary classification of urban versus rural habitats. High-density nations tend to define urban aggregations at a higher threshold than do low-density nations (WRI, 1998). High-density nations would thereby tend to appear more 'rural' and low-density nations would tend to appear more 'urban' than if all used the same classification. Differences in habitat classification may tend to compress the isodar, and may alter the slope if low-density and high-density nations also possess different population sizes. We suspect that neither effect would destroy the highly significant relationship between urban and rural density. Moreover, the logarithmic scale suggests huge differences in urban and rural population sizes that are unlikely to be altered dramatically by differential classification.

Our analyses depend strongly on the quality of the WRI data, on the demographic projections for human populations, and on the consistency of nations maintaining their relative positions with respect to per capita energy consumption. We do not believe that the quality of the data represents a serious impediment to a cautious conservation directive aimed at pre-empting future declines in biodiversity at the global scale. Indeed, others have successfully used global demographic data to evaluate related issues, such as human dynamics in biodiversity hotspots (Cincotta *et al.*, 2000) and human spatial distribution (Cohen and Small, 1998).

Human habitat selection does not, by itself, identify the proximate causal mechanisms threatening the world's biota. Recent studies hint at an intriguing macroecological possibility. Areas of high human population density, both in sub-Saharan Africa (Balmford *et al.*, 2001) and more generally on a world scale (Cincotta *et al.*, 2000), coincide with areas of exceptionally rich biodiversity. Moreover, at least in Africa, dense human populations are also associated positively with areas of high habitat destruction, areas of many endemic species and areas with many threatened species (Balmford *et al.*, 2001). Our results demonstate that the threat intensifies with overall population size, urbanization and the amount of per capita energy consumption, all of which act to increase the value of the human isodar. Effective and preventive global conservation strategies may, therefore, begin by targeting those nations for which isodars of human habitat use predict the greatest urgency for future conservation. We agree with others that interventions need to be based on coordinated priority-driven action plans (e.g. da Fonseca *et al.*, 2000; Mace *et al.*, 2000). Simultaneously, we must work to understand how human behaviours, such as habitat selection, impinge directly, and indirectly, on biodiversity. We believe that such a two-pronged effort has the potential to galvanize international agreements that simultaneously address issues of conservation, human populations and economic disparity.

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APPENDIX 1

Rank order of nations with the greatest difference between 1980 and 2020 population estimates of the probability that the proportions of threatened mammals, birds and higher plants are above the median value for the world's nations [nations are ranked in descending order; nations with high ranks have high increases in probabilities; tests based on WRI (1998) data]

		Difference between 2020 and 1980			
Rank	Nation[a]	Mammals	Birds	Plants	Sum[b]
1	Niger	0.129	0.121	0.085	0.34
2	Uganda	0.116	0.111	0.078	0.30
3	Democratic Republic of Congo	0.112	0.109	0.078	0.30
4	Rwanda	0.109	0.102	0.072	0.28
5	Somalia	0.108	0.102	0.072	0.28
6	Malawi	0.103	0.097	0.068	0.27
7	Madagascar	0.101	0.096	0.067	0.26
8	Nepal	0.099	0.094	0.067	0.26
9	Bhutan	0.097	0.091	0.069	0.26
10	Guatemala	0.097	0.091	0.064	0.25
11	Angola	0.096	0.090	0.063	0.25
12	Mali	0.095	0.090	0.063	0.25
13	Ethiopia	0.090	0.089	0.066	0.25
14	Ghana	0.093	0.088	0.062	0.24
15	Burundi	0.093	0.087	0.061	0.24
16	Burkina Faso	0.091	0.086	0.060	0.24
17	Chad	0.091	0.085	0.060	0.24
18	Islamic State of Afghanistan	0.088	0.084	0.059	0.23
19	Togo	0.086	0.080	0.059	0.22
20	Tanzania	0.085	0.081	0.058	0.22
21	Guinea	0.086	0.080	0.057	0.22
22	Zambia	0.078	0.073	0.052	0.20
23	Papua New Guinea	0.075	0.070	0.051	0.20
24	Benin	0.074	0.069	0.050	0.19
25	Solomon Islands	0.067	0.065	0.061	0.19
26	Senegal	0.070	0.066	0.047	0.18
27	Belize	0.066	0.063	0.053	0.18
28	Côte d'Ivoire	0.069	0.065	0.046	0.18
29	Liberia	0.068	0.063	0.049	0.18
30	Jordan	0.069	0.065	0.045	0.18
31	Pakistan	0.063	0.063	0.049	0.17
32	Kenya	0.065	0.063	0.044	0.17
33	Honduras	0.065	0.061	0.044	0.17
34	Zimbabwe	0.062	0.058	0.041	0.16
35	The Gambia	0.058	0.055	0.047	0.16
36	Central African Republic	0.058	0.055	0.041	0.15
37	Vietnam	0.055	0.055	0.041[c]	0.15
38	Cameroon	0.057	0.054	0.038	0.15
39	Egypt	0.055	0.054	0.039	0.15
40	Nigeria	0.052	0.052	0.040	0.14
41	Guinea-Bissau	0.050	0.048	0.040	0.14
42	Paraguay	0.051	0.048	0.036	0.14
43	South Africa	0.048	0.049	0.040	0.14

Appendix 1—*continued*

Rank	Nation[a]	Difference between 2020 and 1980			
		Mammals	Birds	Plants	Sum[b]
44	Sierra Leone	0.048	0.045	0.033	0.13
45	Swaziland	0.044	0.042	0.037	0.12
46	Haiti	0.047	0.044	0.032	0.12
47	Myanmar	0.046	0.044	0.032	0.12
48	Australia	0.046	0.044	0.031	0.12
49	Costa Rica	0.042	0.039	0.030	0.11
50	El Salvador	0.041	0.038	0.028	0.11
51	Sudan	0.041	0.039	0.028	0.11
52	Nicaragua	0.039	0.037	0.029	0.10
53	Republic of Congo	0.037	0.035	0.028	0.10
54	Gabon	0.036	0.034	0.025	0.09
55	Mozambique	0.036	0.034	0.024	0.09
56	Sri Lanka	0.036	0.034	0.024	0.09
57	Equatorial Guinea	0.029	0.028	0.028	0.09
58	Bangladesh	0.030	0.030	0.024	0.08
59	Panama	0.024	0.023	0.016	0.06
60	Fiji	0.020	0.020	0.018	0.06
61	Peru	0.021	0.020	0.014	0.05
62	Algeria	0.020	0.020	0.015	0.05
63	Malaysia	0.018	0.018	0.014	0.05
64	Saudi Arabia	0.018	0.018	0.012	0.05
65	Mauritius	0.016	0.015	0.013	0.04
66	Albania	0.015	0.014	0.011	0.04
67	Canada	0.015	0.015	0.011	0.04
68	Mexico	0.010	0.011	0.009	0.03
69	Thailand	0.009	0.010	0.009	0.03
70	Libya	0.010	0.010	0.007	0.03
71	Morocco	0.010	0.010	0.007	0.03
72	Surinam	0.010	0.010	0.007	0.03
73	Ecuador	0.009	0.009	0.006	0.02
74	United Arab Emirates	0.007	0.007	0.005[d]	0.02
75	Chile	0.007	0.007	0.005	0.02
76	Tunisia	0.006	0.006	0.004	0.02
77	Mauritania	0.002	0.002	0.002	0.01
78	Guyana	0.002	0.002	0.002	0.005
79	Indonesia	0.001	0.001	0.001	0.003
80	Columbia	0.001	0.001	0.001	0.003
81	United States	−0.001	−0.001	−0.001	−0.003
82	Philippines	−0.003	−0.002	−0.002	−0.01
83	Dominican Republic	−0.004	−0.003	−0.002	−0.01
84	Jamaica	−0.004	−0.003	−0.002	−0.01
85	Venezuela	−0.008	−0.008	−0.005	−0.02
86	Sweden	−0.008	−0.008	−0.006	−0.02
87	Austria	−0.010	−0.009	−0.006	−0.03
88	New Zealand	−0.015	−0.014	−0.010	−0.04
89	United Kingdom	−0.015	−0.014	−0.010	−0.04
90	Greece	−0.019	−0.018	−0.013	−0.05
91	Switzerland	−0.020	−0.018	−0.013	−0.05
92	Iceland	−0.018	−0.017	−0.018	−0.05
93	Norway	−0.023	−0.021	−0.015	−0.06

Appendix 1—*continued*

Rank	Nation[a]	Difference between 2020 and 1980			
		Mammals	Birds	Plants	Sum[b]
94	Ireland	−0.023	−0.021	−0.015	−0.06
95	France	−0.022	−0.022	−0.017	−0.06
96	Italy	−0.022	−0.022	−0.017	−0.06
97	Japan	−0.022	−0.022[e]	−0.018	−0.06
98	Trinidad and Tobago	−0.029	−0.027	−0.020	−0.08
99	Argentina	−0.030	−0.029	−0.020	−0.08
100	Republic of Poland	−0.029	−0.029	−0.022	−0.08
101	Brazil	−0.029	−0.030	−0.026	−0.08
102	Netherlands	−0.034	−0.032	−0.022	−0.09
103	Finland	−0.035	−0.033	−0.023	−0.09
104	Denmark	−0.040	−0.037	−0.027	−0.10
105	Republic of Estonia	−0.037	−0.036	−0.033	−0.11
106	Portugal	−0.042	−0.040	−0.029	−0.11
107	Romania	−0.050	−0.049	−0.037	−0.14
108	Cuba	−0.056	−0.052	−0.039	−0.15
109	Turkey	−0.057	−0.058	−0.046	−0.16
110	Republic of Latvia	−0.074	−0.069	−0.050	−0.19
111	Oman	−0.076	−0.071	−0.051	−0.20
112	Uruguay	−0.077	−0.071	−0.054	−0.20
113	Kuwait	−0.075	−0.071	−0.062	−0.21
114	Bulgaria	−0.081	−0.076	−0.054	−0.21
115	Republic of Lithuania	−0.082	−0.076	−0.054	−0.21
116	Hungary	−0.084	−0.080	−0.057	−0.22
117	Belgium	−0.095	−0.089	−0.067	−0.25
118	Republic of Korea	−0.152	−0.149	−0.111	−0.41

[a] Naming conventions follow those used by the World Resources Institute (WRI, 1998). [b] Sum of all differences; values are rounded to two decimals, there were no tied ranks. [c] Plant diversity in Vietnam assumed to equal 7000 species. [d] The total number of plant species is unknown, but none is listed as threatened. [e] The number of breeding bird species is assumed to be 250.

APPENDIX 2

Rank order of nations (incomplete data) with the greatest difference between 1980 and 2020 population estimates of the probability that the proportions of threatened mammals, birds and higher plants are above the median value for the world's nations [nations are ranked in descending order; nations with high ranks have high increases in probabilities; tests based on WRI (1998) data]

Rank[a]	Nation[b]	Difference between 2020 and 1980		
		Mammals	Birds	Plants
4	Yemen	0.112	0.106	
20	People's Democratic Republic of Laos	0.088	0.082	
23[c]	Tadjikistan			0.056
30	Syrian Arab Republic	0.066	0.065	
32	Cambodia	0.068	0.064	

Appendix 2—*continued*

		Difference between 2020 and 1980		
Rank[a]	Nation[b]	Mammals	Birds	Plants
49	Islamic Republic of Iran	0.043	0.045	
54	Iraq	0.042	0.041	
60[d]	Mongolia	0.036		0.024
65	Israel	0.027	0.025	
75	Democratic People's Republic of Korea		0.012	0.008
85[d]	Bolivia	0.004		0.003
92[c]	Republic of Armenia			−0.007
95[c]	Kazakhstan			−0.012
100[c]	Bosnia and Herzegovina			−0.016
112	Republic of Slovenia	−0.037	−0.034	
114	Czech Republic		−0.037	
117	Slovak Republic		−0.041	
118	Russian Federation	−0.041	−0.042	
119	Republic of Moldova	−0.046	−0.043	
120	Spain	−0.045	−0.043	
122	Republic of Croatia		−0.050	−0.035
124	Germany	−0.057	−0.056	
125	Ukraine		−0.057	−0.044
133	Botswana	−0.082	−0.078	
136	Lebanon	−0.098	−0.091	
137	Republic of Belarus		−0.100	−0.070

[a] Ranked on the basis of threats to avian biodiversity. [b] Only nations with incomplete data are listed. [c] Rank of valid nations with WRI-recorded threats to plants. [d] Rank of valid nations with WRI-recorded threats to mammals.