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Birds and people in Europe

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At a regional scale, species richness and human population size are frequently positively correlated across space. Such patterns may arise because both species richness and human density increase with energy availability. If the species–energy relationship is generated through the ‘more individuals’ hypothesis, then the prediction is that areas with high human densities will also support greater numbers of individuals from other taxa. We use the unique data available for the breeding birds in Europe to test this prediction. Overall regional densities of bird species are higher in areas with more people; species of conservation concern exhibit the same pattern. Avian density also increases faster with human density than does avian biomass, indicating that areas with a higher human density have a higher proportion of small-bodied individuals. The analyses also underline the low numbers of breeding birds in Europe relative to humans, with a median of just three individual birds per person, and 4 g of bird for every kilogram of human.

Keywords: birds; Europe; humans; more individuals hypothesis; population density; body size

1. INTRODUCTION

There is growing evidence that, at regional scales, there are commonly broad positive relationships between the numbers of people living in an area and its species richness; such observations have been made for a range of taxonomic groups (Hunter & Yonzon 1993; Balmford *et al.* 2001; McKinney 2002; Araújo 2003; Chown *et al.* 2003). Species richness and human density arguably tend to be positively correlated because historically, they have responded similarly to spatial variation in the same environmental factors. In particular, at least over low to moderate levels, higher net primary productivity has been proposed to provide a larger resource base, enabling more species to persist in an area (Waide *et al.* 1999; Gaston 2000; Astorga *et al.* 2003; Francis & Currie 2003); richness may, however, decline again at still higher levels of productivity (Balmford *et al.* 2001; Mittelbach *et al.* 2001; Hawkins *et al.* 2003). Areas of higher net primary productivity may also have proved attractive for the establishment of human populations and enabled their subsequent growth. The similarity of the responses exhibited by humans and other biota to productivity may have led to the development of numerous strong parallels between how species richness and human populations are structured in space (Mace & Pagel 1995; Cashdan 2001; Colvard & Foley 2002; Moore *et al.* 2002; Manne 2003), and in how these variables respond to current environmental change (Sutherland 2003).

The most frequently cited argument as to why species richness should increase with the size of the resource base (the species–energy relationship) is that greater energy availability enables more individuals to co-occur, thus allowing more species to attain viable population sizes; the so-called ‘more individuals hypothesis’ (Wright 1983; Rosenzweig & Abramsky 1993; Kaspari *et al.* 2003). This mechanism predicts that the numbers of individuals in an

area and its species richness will be positively correlated, although such a pattern is also consistent with several other possible determinants of species–energy relationships (Evans *et al.* 2004). If energy availability limits population sizes and thus species richness, one expects that, at regional scales, not only will there be a positive relationship between human population size and species richness, but these species should be more abundant and have greater biomass in areas with larger human populations.

The existence of a positive, regional scale relationship between the numbers of individuals of a group of species and the numbers of people in an area is, in general, extremely difficult to test. However, positive species–energy relationships have been documented for birds in Europe, although these sometimes contain a negative phase (Lennon *et al.* 2000; Araújo 2003; Hawkins *et al.* 2003), and estimates of the population sizes of breeding birds in European geopolitical units have recently been produced. The opportunity thus exists to make a first approximation as to the existence and form of the relationship between the number of birds and people. In so doing, we can also test the suggestion that, in much of the world, there are very few breeding birds relative to the numbers of people (Gaston *et al.* 2003).

Throughout this paper, we focus on regional extents and data resolutions. Relationships between numbers of wild birds and people at local scales may be quite different, with, unsurprisingly, severe conflicts between the two having often been documented (e.g. BirdLife International 2000; Marzluff *et al.* 2001; Sinclair *et al.* 2002).

2. METHODS

Analyses were based on avian population estimates derived from BirdLife International/European Bird Census Council (2000), which have been employed in several recent macroecological analyses (e.g. Gregory *et al.* 1998; Gregory 2000; Gaston 2002; Gaston *et al.* 2003); for a discussion of the strengths and weaknesses of these data see Gregory *et al.* (1998), BirdLife International/European Bird Census Council (2000) and

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Gregory (2000). These data comprise estimates of the minimum and maximum number of breeding pairs or individuals of each bird species for each of several geopolitical entities (principally countries): Albania, Andorra, Austria, Azores, Belarus, Belgium, Bulgaria, Canary Islands, Croatia, Cyprus, Czech Republic, Denmark, Estonia, Faroe Islands, Finland, France, Germany, Gibraltar, Greece, Greenland, Guernsey, Hungary, Iceland, Isle of Man, Italy, Jersey, Latvia, Liechtenstein, Lithuania, Luxembourg, Madeira, Malta, Moldova, The Netherlands, Norway, Poland, Portugal, Republic of Ireland, Romania, European Russia, Slovakia, Slovenia, Spain, Svalbard, Sweden, Switzerland, Turkey, Ukraine and the UK. Most of these data were collected between 1985 and 1995, but many were subsequently updated. Figures are missing for a few species in a few units, but principally for several common species in Poland, which was therefore dropped from the analyses; other omissions will not markedly influence the results reported. European Russia was also excluded, as we could not readily obtain data on human population size, because the edges of this region do not coincide with any political entities. All abundance estimates were converted to numbers of individuals, and marine species were excluded, following the scheme of Gregory *et al.* (1998). Such data are not available for units at smaller spatial scales and our analyses incorporate all available estimates of total avian abundance from geopolitical units in the western palaeartic/European biogeographical region. Greenland is the only unit that we consider that is sometimes classified in a separate region, the Nearctic (Cramp *et al.* 1977–1994; Hagemeyer & Blair 1997; Olson *et al.* 2001); we thus perform analyses on data that include and exclude Greenland.

Following Tucker & Heath (1994), five categories of conservation concern were distinguished: (i) SPEC 1, species of global conservation concern; (ii) SPEC 2, species not of global concern, with unfavourable conservation status and concentrated in Europe; (iii) SPEC 3, species not of global concern, with unfavourable conservation status in Europe and not concentrated in Europe; (iv) SPEC 4, species not of global concern, with favourable conservation status in Europe and concentrated in Europe; and (v) non-SPEC, species not of global concern, with favourable conservation status in Europe and not concentrated in Europe. Species categorized as SPEC 1, SPEC 2 or SPEC 3 were considered to be of European conservation concern.

Mean body masses of species were obtained principally from Cramp *et al.* (1977–1994). The biomass of each bird species (in kilograms), in each geopolitical unit, was calculated as the product of the geometric mean population estimate and mean body mass. Intraspecific geographical variation in body masses is common in Europe, but is of minor magnitude, relative to interspecific variation (Cramp *et al.* 1977–1994); it is thus unlikely to significantly influence the results reported.

Estimates of the area of each geopolitical unit, and of its human population size (as of July 2003) were obtained principally from <http://www.cia.gov/cia/publications/factbook>, with the gaps, predominantly for the smaller units, being filled from a diversity of sources. We used the ice-free area of Greenland in our analyses, calculated from Loveland *et al.* (2000). We used the geometric mean estimates of avian population sizes to calculate the density of birds (per square kilometre) in each unit and the density of avian biomass (kilograms per square kilometre). The human biomass in each unit was calculated as the total biomass of adults and children, defining the latter as people less than 15 years old. We assumed an even sex ratio, a mean adult

male mass of 68.2 kg, a mean adult female mass of 55.0 kg and child masses of half their respective adult values. We obtained data on the proportion of the population under 15 years from Haub (2003). Mass estimates were derived from a global analysis of human body size (Jungers 1985) and, as Europeans are probably heavier than the global mean, are likely to generate underestimates of human biomass in Europe, making our analyses of anthropogenic impacts slightly conservative.

Following logarithmic transformations, all variables were normally distributed (Ryan–Joiner *W*-test $p > 0.05$) and we use these transformed variables in all our analyses, which were conducted using SAS, v. 8.2. The mean values that we report are calculated from untransformed data and presented ± 1 s.e.m. Our general approach is to perform univariate tests and then to construct minimum adequate models (MAMs), using a forwards selection procedure, that control for potentially confounding variables. Predictors were retained in the MAM if they were statistically significant ($p < 0.05$), as assessed by *F*-ratios. When investigating factors that influenced avian abundance we repeated the analyses using three different response variables: (i) the sum of the minimum population size of each species; (ii) the summed maximum population size; and (iii) the summed geometric mean population size.

We conducted two sets of analyses; the first assumed independent errors and used general linear models (GLMs). Spatial autocorrelation may, however, systematically invalidate the assumption of independent errors, distorting classical tests of association and rendering correlation coefficients, regression slopes and associated significance tests misleading (Clifford *et al.* 1989; Cressie 1991; Legendre 1993; Lennon 2000; Legendre *et al.* 2002). To avoid this, a second set of analyses was conducted using the PROC MIXED procedure to implement spatial correlation models (Littell *et al.* 1996). For each response variable we assessed which of six spatial covariance structures (spherical, exponential, gaussian, linear, log linear and power) gave the best fit to the null model and tested whether our data exhibited significant spatial autocorrelation, as assessed by log likelihood ratio tests (table 1).

3. RESULTS AND DISCUSSION

Across Europe, there was a strong, positive and statistically significant linear relationship between the number of breeding bird species and human population size in geopolitical units, in univariate tests based on both independent error models and spatial ones (figure 1; table 2). This relationship remained significant in independent error models that controlled for the areas of the different units, but not in spatial ones (table 2).

At the scale of 50 km grid cells, Araújo (2003) found that avian species richness across Europe is only very weakly positively correlated with human population density, although the species richness of plants, amphibians and reptiles, and mammals exhibited stronger positive relationships. The contrast between our results and those of Araújo (2003) may arise from: (i) differences in the spatial extent of our analyses (for example, unlike Araújo (2003), we exclude some former Soviet bloc countries for which data were not available); and (ii) the larger spatial grain of our analyses. Our detection of a stronger relationship may therefore reflect a general, but not invariant trend, documenting more significant relationships at larger scales (Manne 2003). However, when we

Table 1. Results of log-likelihood ratio tests that assess the extent of spatial autocorrelation.

response variable	Greenland included		Greenland excluded	
	best-fitting spatial structure	test statistics χ^2, p	best-fitting spatial structure	test statistics χ^2, p
richness: all species	spherical	26.4, < 0.0001	spherical	25.17, < 0.0001
richness: SPEC species	exponential	24.5, < 0.0001	exponential	23.21, < 0.0001
abundance: all species max.	Gaussian	3.0, 0.08	Gaussian	2.89, 0.088
abundance: all species min.	Gaussian	2.9, 0.09	Gaussian	2.21, 0.088
abundance: all species mean	Gaussian	3.0, 0.08	Gaussian	2.93, 0.087
abundance: mean SPEC species	exponential	3.0, 0.08	Gaussian	3.61, 0.057
avian biomass: all species	Gaussian	3.8, 0.05	Gaussian	3.74, 0.053
avian biomass: SPEC species	Gaussian	6.2, 0.01	Gaussian	6.08, 0.014
avian density: all species	exponential	12.6, < 0.0001	exponential	7.88, 0.005
avian density: SPEC species	spherical	29.8, < 0.0001	exponential	12.61, 0.0004
avian biomass density: all species	Gaussian	18.9, < 0.0001	Gaussian	14.99, 0.0001
avian biomass density: SPEC species	exponential	21.5, < 0.0001	exponential	10.55, 0.0012

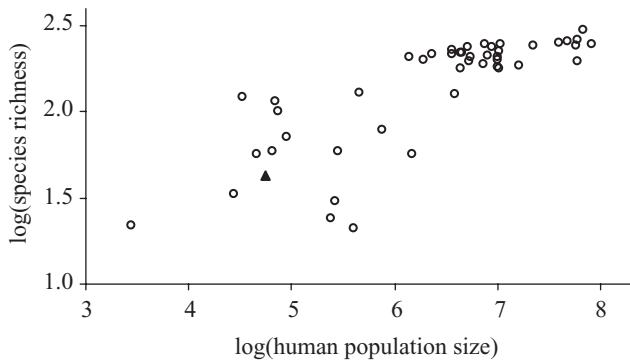


Figure 1. The relationship between the species richness of the breeding avifauna and the human population size in Western Palaearctic geopolitical units. The black triangle represents Greenland (which is sometimes considered part of the Nearctic region).

control for spatial autocorrelation and area we do not find a significant relationship between avian species richness and human density, which concurs more closely with the findings of Araújo (2003), although the latter study did not control for spatial autocorrelation.

Avian abundance in geopolitical units also exhibited a strong and statistically significant positive correlation with the numbers of people, regardless of whether mean, minimum or maximum population estimates were used; these results remained significant when controlling for area in independent error models and spatial ones, and did not change when Greenland was excluded from the data (table 2). The regression, based on a spatial MAM that used mean population estimates and included Greenland, had an estimated slope of 0.535 ± 0.067 (all estimates of slopes presented are based on analyses that include Greenland, as excluding it did not significantly change the estimates). Avian biomass was also positively correlated with human abundance (table 2), albeit with a shallower slope (0.395 ± 0.075). Although this is not surprising given a strong positive correlation between avian abundance and biomass (GLM: $r^2 = 0.925, p < 0.0001$; spatial $p < 0.0001$), it is interesting to note that the slope of the latter relationship does not differ from unity (spatial model 1.060 ± 0.045); such a slope is expected if body mass did

not influence the manner in which energy was subdivided between species.

These positive correlations between avian species richness, total abundance and biomass with human population density are predicted to occur if positive correlations arise between human population size and a taxon's species richness as a consequence of: (i) energy availability limiting species richness by restricting population size, as described by the more individuals hypothesis; and (ii) that human population size and species richness respond similarly to energy availability. The slope of the relationship between avian population size and human population size was steeper in an analysis confined to species of conservation concern (0.734 ± 0.083 : spatial model controlling for area) compared with one that used data from all species. This variation may arise because species of conservation concern respond more strongly to energy availability than unthreatened species. However, this appears to be unlikely as the regression of biomass of threatened bird species against human population size had a similar slope (0.399 ± 0.078) to the regression that used data from all species. Total avian abundance increased more rapidly with human population density than does avian biomass, the regressions have steeper slopes, indicating that areas with high human densities contain a greater proportion of small-bodied birds. Anthropogenic influences on the shape of body-size frequency distributions for given taxa have seldom been explored explicitly (but see Gaston & Blackburn 2003), but are not unexpected, given the tendency for larger-bodied species to have life-history traits that render them more vulnerable to extinction than similar smaller-bodied species (Pimm *et al.* 1988; Foufopoulos & Ives 1999; Jennings *et al.* 1999; Cardillo 2003; but see Brashares 2003; Roff & Roff 2003).

Using the mean population size estimates averaged across all geopolitical units, there are 9.99 ± 4.0 breeding birds per person, but the median is much lower, 3.02. The highest ratios are for Greenland, 187.8, and Svalbard, 33.9; although in the former there are large uncertainties in bird estimates and many species are suffering severe declines (Hansen 2002). The lowest ratio is for Madeira, 0.26, although this may be partly an artefact generated by the lack of population estimates for a few species in this

Table 2. Results of univariate and multivariate regressions, which control for area, of the relationship between human population size and the structure of avian assemblages in European geopolitical units.

(When significant, all predictors have positive effects with $p < 0.0001$, except when indicated with ** when $p < 0.001$. Smaller Akaike Information Criteria (AIC) values indicate a better model fit. n.s., not significant; n.a., not applicable.)

response	test	Greenland included			Greenland excluded		
		human $F_{1,45}$	area $F_{1,45}$	model fit	human $F_{1,44}$	area $F_{1,44}$	model fit
richness: all species	GLM univariate	84.01	—	$r^2 = 0.651$	76.63	—	$r^2 = 0.635$
	GLM univariate	—	33.94	$r^2 = 0.430$	—	44.85	$r^2 = 0.505$
	GLM MAM	84.01	n.s.	$r^2 = 0.651$	76.63	n.s.	$r^2 = 0.635$
	spatial univariate	82.58	—	AIC = -31.5	80.70	—	AIC = -31.2
	spatial univariate	—	106.75	AIC = -39.0	—	107.25	AIC = -39.4
	spatial MAM	n.s.	106.75	AIC = -39.0	n.s.	107.25	AIC = -39.4
richness: SPEC species	GLM univariate	112.07	—	$r^2 = 0.714$	103.23	—	$r^2 = 0.701$
	GLM univariate	—	36.52	$r^2 = 0.448$	—	47.03	$r^2 = 0.517$
	GLM MAM	112.07	n.s.	$r^2 = 0.714$	103.23	n.s.	$r^2 = 0.701$
	spatial univariate	127.37	—	AIC = -23.5	127.69	—	AIC = -23.4
	spatial univariate	—	167.74	AIC = -30.8	—	166.79	AIC = -31.4
	spatial MAM	—	167.74	AIC = -30.8	n.s.	166.79	AIC = -31.4
abundance: all species mean	GLM univariate	151.15	—	$r^2 = 0.771$	195.17	—	$r^2 = 0.816$
	GLM univariate	—	218.09	$r^2 = 0.830$	—	231.8	$r^2 = 0.840$
	GLM MAM	46.19	76.97	$r^2 = 0.917$	54.5	41.55	$r^2 = 0.919$
	spatial univariate	143.82	—	AIC = 89.2	186.20	—	AIC = 78.9
	spatial univariate	—	218.09	AIC = 75.0	—	231.80	AIC = 71.5
	spatial MAM	46.19	76.97	AIC = 46.2	41.55	54.50	AIC = 44.9
abundance: all species min.	GLM univariate	172.44	—	$r^2 = 0.793$	187.37	—	$r^2 = 0.810$
	GLM univariate	—	178.85	$r^2 = 0.800$	—	219.50	$r^2 = 0.833$
	GLM MAM	54.79	57.70	$r^2 = 0.910$	37.91	49.14	$r^2 = 0.911$
	spatial univariate	164.76	—	AIC = 83.2	178.78	—	AIC = 78.8
	spatial univariate	—	178.85	AIC = 80.8	—	219.50	AIC = 71.8
	spatial MAM	54.79	57.70	AIC = 47.8	37.91	49.14	AIC = 47.1
abundance: all species max.	GLM univariate	120.01	—	$r^2 = 0.727$	189.45	—	$r^2 = 0.812$
	GLM univariate	—	221.95	$r^2 = 0.831$	—	216.02	$r^2 = 0.813$
	GLM MAM	28.24	72.87	$r^2 = 0.897$	38.61	47.90	$r^2 = 0.911$
	spatial univariate	195.36	—	AIC = 93.5	218.39	—	AIC = 77.9
	spatial univariate	—	212.94	AIC = 75.4	—	207.36	AIC = 74.6
	spatial MAM	27.93	73.41	AIC = 56.5	38.04	48.67	AIC = 49.9
abundance: mean SPEC species	GLM univariate	192.16	—	$r^2 = 0.810$	199.19	—	$r^2 = 0.819$
	GLM univariate	—	183.42	$r^2 = 0.803$	—	246.35	$r^2 = 0.848$
	GLM MAM	68.01	63.88	$r^2 = 0.923$	44.07	60.95	$r^2 = 0.925$
	spatial univariate	315.70	—	AIC = 84.5	189.17	—	AIC = 91.4
	spatial univariate	—	will not converge	n.a.	—	246.35	AIC = 83.0
	spatial MAM	64.86	53.90	AIC = 59.3	44.07	60.95	AIC = 54.9
avian biomass: all species	GLM univariate	88.75	—	$r^2 = 0.891$	102.61	—	$r^2 = 0.700$
	GLM univariate	—	267.12	$r^2 = 0.856$	—	295.12	$r^2 = 0.870$
	GLM MAM	13.51	90.21	$r^2 = 0.890$	8.47**	76.05	$r^2 = 0.892$
	spatial univariate	1277.46	—	AIC = 79.0	1226.6	—	AIC = 73.1
	spatial univariate	—	614.91	AIC = 54.8	—	591.72	AIC = 50.0
	spatial MAM	17.90	75.56	AIC = 42.7	12.38**	60.24	AIC = 42.0
avian biomass: SPEC species	GLM univariate	94.25	—	$r^2 = 0.677$	109.24	—	$r^2 = 0.713$
	GLM univariate	—	321.09	$r^2 = 0.877$	—	365.44	$r^2 = 0.893$
	GLM MAM	16.58	115.26	$r^2 = 0.911$	10.11**	89.98	$r^2 = 0.913$
	spatial univariate	223.13	—	AIC = 98.2	218.41	—	AIC = 92.9
	spatial univariate	—	286.05	AIC = 66.5	—	325.87	AIC = 60.4
	spatial MAM	17.26	104.74	AIC = 55.0	10.70**	89.98	AIC = 53.7

species-poor geopolitical unit. Malta has the second lowest ratio, 0.27, and Italy also has a low ratio, 1.02. Although hunting occurs more widely, these two countries are known for their intense hunting pressure with huge numbers of birds, the bulk on migration, killed per annum (Fenech 1993; Heath & Evans 2000). It is thus interesting to note that the mean ratio of these two countries is

significantly lower than that of all other countries, even when Greenland is excluded (95% confidence intervals Italy and Malta -0.086 to 1.378; other countries 3.944 to 5.702); although many other factors may influence these ratios, hunting pressure could be important.

The UK has a ratio of 2.11, which places it close to the middle of a 'league table' of ratios. In most countries,

Table 3. Estimated numbers of individuals of wild breeding birds (non-marine), wild mammals (pre-breeding population), livestock, pets and humans in the UK.

	numbers	year	source
wild birds	126 541 000 ^a	1985–1995 ^b	BirdLife International/European Bird Census Council (2000)
wild mammals	284 956 000 ^c		Harris <i>et al.</i> (1995)
livestock			
cattle	11 519 000	1998	http://earthtrends.wri.org/index.cfm
sheep	44 471 000	1998	http://earthtrends.wri.org/index.cfm
equines	172 600	1998	http://earthtrends.wri.org/index.cfm
swine	8 146 000	1998	http://earthtrends.wri.org/index.cfm
chickens	152 886 000	1998	http://earthtrends.wri.org/index.cfm
turkeys	12 408 000	1998	http://earthtrends.wri.org/index.cfm
ducks	2 505 000	1998	http://earthtrends.wri.org/index.cfm
total livestock	232 107 600		
pets			
cats	7 500 000	2002	http://www.pfma.com/petownership.htm
dogs	6 100 000	2002	http://www.pfma.com/petownership.htm
total pets	13 600 000		
humans	59 657 000	2002	United Nations Development Programme <i>et al.</i> (2003)

^a Geometric mean estimate (see § 2).

^b With subsequent corrections (see § 2).

^c Britain only.

the numbers of birds per person are extremely low and the extent to which humans dominate European ecosystems is further emphasized by considering ratios of avian biomass to human biomass. These ratios have a mean of 0.035 ± 0.023 (bird kilogram to human kilogram) and a median of 0.0042; when Greenland is excluded the respective figures are 0.031 ± 0.023 and 0.0039. Malta has the lowest ratio (0.000 15), again suggesting that intense hunting pressure affects this country's avifauna, and the highest ratios are in relatively pristine areas (Greenland, 0.2171; Svalbard, 1.0732). These biomass ratios are very low, but are probably overestimates, as we assume that the mean mass of a European person is equal to the global mean; in reality Europeans are probably heavier.

Global avian abundance has probably declined by at least 20–25% since agriculture became widespread (Gaston *et al.* 2003) and European human population densities were, historically, much lower (Klein Goldewijk 2001). Therefore, the ratios that we report were almost certainly much higher in the past. The current domination of European ecosystems by humans is, of course, even higher than our ratios suggest, as we do not consider, for example, the large numbers and biomass of livestock and other species that are commensal with humans. In the UK, one of the only regions for which detailed data are available, the numbers of breeding wild birds is outnumbered by the numbers of chickens alone, and there is one domestic cat for every 17 wild birds (table 3).

The historical declines in the ratios of wild birds to human populations are likely to continue throughout much of Europe for three reasons. First, there is often a temporal lag between the modification of habitat suitability and a biota's response to it (Dickman *et al.* 1999; Chamberlain *et al.* 2000), so even if habitat alteration

ceased today, many species are likely to continue to exhibit population declines. Second, many bird species (particularly, but not exclusively, farmland specialists) have exhibited widespread and severe population declines that are anticipated to continue and to become more widespread as a consequence of the expansion of intensive western style agriculture into eastern Europe (Tucker & Heath 1994; Donald *et al.* 2001; Robinson & Sutherland 2002). Although some species are increasing in abundance, the magnitude of such increases is small relative to the size of population declines (Tucker & Heath 1994; Raven *et al.* 2003). Third, by 2050, human populations in northern Europe are anticipated to increase by 6% through internal growth, and may grow even more as a consequence of immigration; in southern Europe, although birth rates are falling, immigration may still lead to increased human population sizes in many countries (Haub 2003).

The extremely small values of the ratios of birds to humans and our prediction that such values will continue to fall raises several fundamental points of applied importance. First, such ratios may provide a useful index of sustainability, of the form advocated by Balmford *et al.* (2003), as they encapsulate short-term biodiversity trends in a single measure that is simple to interpret. Second, they strongly support assertions that humans appropriate an increasingly large and disproportionate amount of the Earth's net primary productivity (Vitousek *et al.* 1986; Haberl *et al.* 2001, 2002; Pimm 2001; Rojstaczer *et al.* 2001). Third, our prediction of declining ratios suggests that humans may have progressively fewer opportunities for first-hand experience of other life-forms; however, such contacts may be vital in stimulating an appreciation of the natural world and the desire to conserve it (Collar 2003; Pyle 2003).

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