

How many birds are there?

KEVIN J. GASTON*

Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

TIM M. BLACKBURN

NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, UK

Received 9 May 1996; revised and accepted 6 August 1996

Attempts to assess the magnitude of global biodiversity have focused on estimating species richness. However, this is but one component of biodiversity, and others, such as numbers of individuals or biomass, are at least as poorly known and just as important to quantify. Here, we use a variety of methods to estimate the global number of individuals for a single taxon, birds. The different methods yield surprisingly consistent estimates of a global bird population of between 200 billion and 400 billion individuals (1 billion = 10^9). We discuss some of the implications of this figure.

Keywords: biodiversity; birds; populations.

‘It is rather difficult to realise what enormous numbers of animals there are everywhere, not only in species but in number of individuals of each species.’
Charles Elton (1927)

Introduction

The global magnitude of extant biodiversity is poorly understood. In the context of species richness, in particular, this fact has been much lamented. The under-developed state of listings of the world’s species has been contrasted with the more advanced catalogues of stars and galaxies (May, 1990), and the lack of a definitive estimate of the overall number of species has been contrasted with estimates of the number of stars of the Milky Way (Wilson, 1985). The differences are all the more lamentable given that (effectively) all the stars we know of today will still be around to study in 100 years time, yet the same is demonstrably untrue of species.

The general lack of knowledge about the overall number of species with which we share the planet has, in part, engendered various attempts to estimate these numbers for particular taxa, regions and habitat types. The estimates have of necessity been indirect, extrapolating information from small areas or well-known taxa to larger areas or more poorly known taxa. To give an extreme example, Erwin (1982) used information on the species richness of beetles in a few specimens of a single species of rain forest tree to estimate the insect richness of the entire tropical region. Other extrapolations have used the relationship between number of species and body size (May, 1990), ratios of described to undescribed species encountered in samples (Hodkinson and Casson, 1991), the judgments of taxonomists as to the richness of the groups they study (Gaston, 1991), ratios of insect to plant taxa in different countries (Gaston, 1992), and the proportions of species in various taxa found in different biogeographic regions (Gaston and Hudson, 1994).

*To whom correspondence should be addressed.

Some consensus over the likely bounds to global species richness has resulted, with a working estimate of around 13.5 million, albeit with the (highly unlikely) upper and lower estimates differing by roughly two orders of magnitude (3.5–111.5 million species; Heywood, 1995).

Although attention has been focused on species richness there are other dimensions to global biodiversity which are at least as poorly known, may perhaps be just as important to quantify, and about which the failure to quantify may be equally lamentable. The total number of individual organisms in the world, for example, has been a largely ignored statistic. Nonetheless, just as the species, the individual is regularly identified as a level in hierarchical schemes of the components of biodiversity (e.g. Heywood, 1995). Indeed, it is one of the few entities that is frequently represented in more than one hierarchy in schemes that recognize multiple hierarchies of biodiversity (e.g. genetic, organismal and ecological diversity). If, as some have maintained, no level of biodiversity is any more fundamental than any other, then it would seem as essential to ask about global numbers of individuals as about global numbers of species.

At a regional scale, the number of individual organisms represents a broad brush expression of biodiversity in that it explicitly ignores differences in species and higher level taxonomic affinities; two areas may have equivalent numbers of individuals, but widely divergent species or taxonomic composition. However, on average, the number of individuals does tend to scale positively with measures of taxonomic diversity. Thus, the total numbers (or biomass) of individuals and the species richness of a taxon in assemblages are related both theoretically and empirically (e.g. Kobayashi and Kimura, 1994). Moreover, species richness gradients are often suggested to arise through gradients in productivity or the energy available to species in different areas (e.g. Wright *et. al.*, 1993). If true, it implies that richness patterns cannot be considered in isolation from the biomass of those species, because it is this quantity that available energy actually limits (Blackburn and Gaston, 1996). Estimating the number of individuals is, in this sense, a first step along the road to a quantitative measure of diversity.

The number of individual organisms would actually seem more amenable to assessment than the number of species. Counting individuals has a number of practical advantages over counting species (accepting that clonal species create some particular problems). First, the need to classify individuals to species disappears, avoiding one of the major constraints on the study of biodiversity, the paucity of taxonomic expertise (Gaston and May, 1992). Misidentifications do not inflate or deflate the numbers of individuals, and the amount of specialized work required to estimate one key component of the biodiversity of an area is drastically reduced. Overlooking rare species may significantly depress the species richness of an area, but will have relatively little effect on the estimate of the number of individuals. Second, it will generally be easier to census areas for numbers of individuals than for numbers of species. Provided the major habitat divisions of an area are all visited to obtain estimates of how numbers of individuals vary between them, complicated or fine scale patterns of species replacement within those areas can be ignored. Also, ecologically similar but widely separated sites are likely to differ markedly in their species composition, but perhaps less so in the number of individuals they support. Third, the number of individuals in a small area can more easily be multiplied up to give the number of individuals in a large area than can the number of species. The complications of the non-linearities of species-area relationships are avoided.

As far as we are aware, the only explicit attempt to calculate the overall number of individuals in a large taxon is that of Williams (1960). He estimated that the global insect fauna consists of around 1×10^{18} animals, based in part on the assumption that the global insect fauna is around three million species, which is probably unrealistically low.

In this paper, we follow the example Williams set, by estimating the global number of individual animals in a taxon, Aves. The relatively good information available for birds means that we can derive estimates using a variety of methods. For all methods, we consider numbers of landbirds first, and subsequently address the question of how many seabirds to add to that total.

Numbers fluctuate both through and between seasons. We ignore such details and seek order of magnitude estimates only. To some (unknown) extent fluctuations in different parts of the globe will be out of synchrony, so that fluctuations in the overall total number of individuals will be less than fluctuations in regional totals.

Method I

The first method is based on estimates of the overall density of birds at local study sites, and scaling these up to the area of the globe. The number of local sites at which bird densities have been determined is enormous. Most studies report densities by species, which could potentially be summed to give the total number of individuals in the area. Instead, however, we consider the densities reported in just a single paper – that of Terborgh *et al.* (1990) on the densities of forest birds. This paper summarizes estimates of the total number of individuals in a square kilometre of seven different forests from five continents (Table 1). One could debate at length the appropriateness of the choice of studies which the authors use, but we shall accept these at their face value.

Table 1. Estimates of the local density of individual birds (number/km²) of all species at seven forest sites on five continents. Three estimates are from temperate latitudes, and four from the tropics. All data are from Terborgh *et al.* (1990)

Site	Region	Individuals/km ²
	<i>Temperate</i>	
Hubbard Brook	North America	2000
Białowieża I	Europe	1240
Białowieża II	Europe	700
	temperate mean	1313.3
	<i>Tropical</i>	
Cocha Cashu	South America	1920
Panama	Central America	3640
French Guiana	South America	760
Gabon	Africa	3690
New Guinea	Oceania	6900
	tropical mean	3382
	tropical mean excluding New Guinea	2502.5
	overall mean	2606.25
	overall mean excluding New Guinea	1992.9

We used these figures to generate estimates of the mean number of individuals in an average square kilometre of land, and in an average square kilometre in the tropical and temperate regions separately. Terborgh *et al.* (1990) question the accuracy of the high figure for the density of birds in New Guinea, because it potentially suffers from distortions due to the small plot size on which it is based. Whilst it has been suggested to us that the New Guinea figure may not actually be atypical, we calculated the tropical and global mean density twice, once including and once excluding this figure (Table 1).

To obtain estimates for the number of individual birds globally, we multiplied the square kilometre densities in Table 1 by estimates of total land area for the globe. An approximate figure for this area is 149 million square kilometres. However, around 13 million square kilometres are under ice. We assumed this area houses no landbirds, and excluded it from calculations. Assuming a mean density of 2606.25 birds per square kilometre gives a global total of 3.54×10^{11} individual landbirds. With the data from New Guinea excluded, that total is reduced to 2.71×10^{11} birds.

The above estimates ignore the division of land between tropical and temperate areas. These regions maintain quite different bird densities (Table 1). We therefore considered them separately, obtaining estimates of their areas from Tables 18.1 and 29.6 in Groombridge (1992). Table 18.1 gives the areas covered by tropical and temperate habitat types, from which we calculated that the tropics cover 74 million square kilometres, and the temperate zone 60 million square kilometres. Table 29.6 indirectly gives the land areas of the following seven regions: Europe, USSR (as was), Asia (excluding the USSR), Oceania, Nearctic (North and Central America), South America, and Africa. Assuming that Asia, Africa and South America comprise the tropics and that Europe, the USSR, the Nearctic and Oceania comprise the temperate region, gives estimates of land areas for these regions of 75.7 and 60.4 million square kilometres respectively. In subsequent calculations we used a tropical area of 75 million square kilometres, and a temperate area of 60 million square kilometres.

Combining these figures with those in Table 1 gives estimates of 7.88×10^{10} individual birds in temperate areas, and either 2.54×10^{11} (including the New Guinea data) or 1.88×10^{11} (excluding it) in tropical areas. Summed across regions, the total number of landbirds is 2.67 or 3.33×10^{11} individuals.

Method II

The second method involves extrapolation of estimates for the number of birds in a geographic region. Such estimates were available for four countries and two continents. We deal with the political and geographic areas separately.

Table 2 gives estimates for the numbers of individual birds in the USA, Britain, Sweden, and Finland, together with the areas of these countries, and the sources of the estimates. The estimates for Britain and Sweden exclude introduced and stocked species, as well as seabirds. These abundances yield densities of between 184 (Finland) and 608 (USA) birds per square kilometre. Assuming a land area of 136 million square kilometres, this gives a range of estimates of 2.5 to 8.27×10^{10} individuals globally, with a mean of 5.05×10^{10} individuals. If instead we sum the numbers of individuals and the extents of the different countries and divide the former by the latter, we obtain an estimate of 574 birds per square kilometre, which gives a global estimate of 7.8×10^{10} individuals.

Table 3 gives the same information as Table 2, but with estimates for the numbers of individual birds on continents. Averaging these estimates gives a mean of 1432 birds per

Table 2. Estimates for the number of individual birds in different countries, together with the area of the country, the mean density of birds calculated for a square kilometre of the country from the previous two figures, and the source for the data

Country	Number of individuals		Area (km ²)	Individuals /km ²	Source
USA	5 700 000 000		9 373 000	608	Rosenzweig (1995)
Britain	114 000 000	breeding	230 600	494	Marchant <i>et al.</i> (1990)
Sweden	90 000 000	breeding	450 000	200	Ulfstrand & Hogstedt (1976)
Finland	62 000 000	breeding	337 000	184	Merikallio (1958)
			Mean	371.5	

square kilometre, which extrapolates to 1.95×10^{11} individual birds. Summing the numbers of individuals and the extents of the two areas, we obtain an estimate of 1600 birds per square kilometre, yielding a global estimate of 2.18×10^{11} individuals. Alternatively, assuming that the African figure is representative of tropical regions and the Nearctic estimate representative of temperate regions, multiplying up by the land areas of these regions (as calculated above) gives a value of 2.08×10^{11} individual birds.

Method III

The third method uses the same data as the second, but a different form of extrapolation. We regressed the estimated number of individual birds in countries and on continents against the areas of those geographic units, with both axes logarithmically (base 10) transformed (Fig. 1). Substituting global land area ($\log 136$ million = 8.134) into the regression equation gives a global estimate of 2.21×10^{11} individual birds.

Method IV

The fourth method uses allometric scaling of species densities to produce an expected range of densities for species based on their body sizes. A number of studies have reported the relationship between abundance and body size in birds (e.g. Carrascal and Tellería, 1991; Blackburn *et al.*, 1994; Cotgreave and Harvey, 1994; Tellería and Carrascal, 1994; Cotgreave, 1995). Most of these studies are unhelpful here in that they do not report the full regression equation (the intercept is usually omitted), or they deal in population sizes

Table 3. Estimates for the number of individual birds on different continents, together with the area of the continent, the mean density of birds calculated for a square kilometre of the continent from the previous two figures, and the source for the data

Continent	Number of individuals	Area (km ²)	Individuals /km ²	Source
Africa	72 500 000 000	30 300 000	2393	Brown <i>et al.</i> (1982)
Nearctic	10 000 000 000	21 250 000	471	Preston (1948)
		Mean	1432	

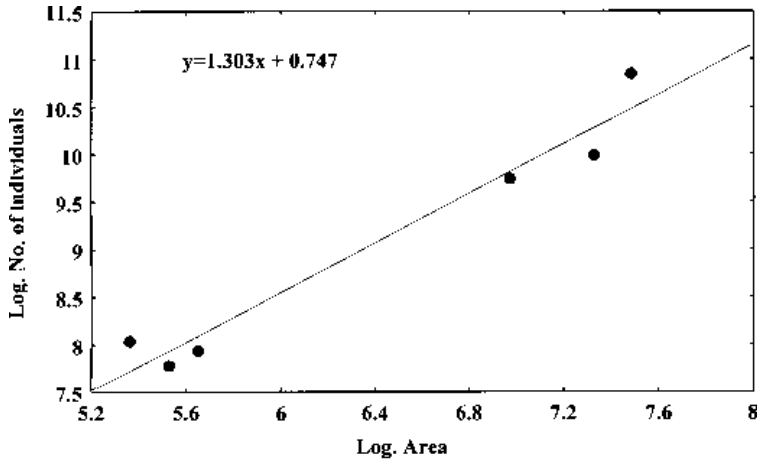


Figure 1. The relationship between \log_{10} number of individuals in a geographical region and the \log_{10} land area (km^2) of that region ($r^2 = 0.96$, $n = 6$, $p = 0.008$).

rather than densities. We used the regression equation, given by Juanes (1986), for 564 species of birds:

$$D = 1.96 - 0.49M$$

where D is \log_{10} transformed density (per square kilometre) and M is \log_{10} transformed body mass (g). We substituted data on the body masses of 5428 species of landbird (Dunning, 1992) into this equation, to give the distribution of densities expected on the basis of those masses. We have shown elsewhere (Blackburn and Gaston, 1994) that with respect to body size these species are a random subset of the birds of the world. The mean density of landbird species in this subset is 18.3 individuals per square kilometre. However, because the density distribution is highly right-skewed, even on logarithmic axes (skewness = 0.735), we used the median density of 17.22 km^{-2} instead.

To convert the median density of bird species into the total number of birds per square kilometre requires an estimate of the average number of species coexisting in a square kilometre. Terborgh *et al.* (1990) found 245 species resident in 97 hectares at Cocha Cashu, Peru. The temperate forests they discuss house far fewer: 24 species in 10 hectares in an average year at Hubbard Brook, and 40 species in a square kilometre at Białowieża. Taking 40 and 245 species as reasonable numbers for temperate and tropical regions, respectively, gives densities of 688.8 and 4218.9 individuals per square kilometre. Multiplying each by the land area of the region results in a global estimate of 3.58×10^{11} individuals.

Seabirds

Thus far we have ignored seabirds. It is much more problematic to derive density estimates for these species than it is for landbirds, because the area to use to calculate densities is unclear. However, having obtained estimates for the total number of individual landbirds, we can estimate the number of seabirds if we calculate the ratio between numbers of seabirds and landbirds. Marchant *et al.* (1990) give estimates of the numbers of both land

and seabirds breeding in Britain. We have already used the number of landbirds in Methods II and III (Table 2). The number of individual seabirds (auks, terns, gulls, skuas, sea ducks and grebes) is 6.67×10^6 . Seabirds therefore comprise 5.5% of the British avifauna. If we assume that this relationship holds globally, then the number of individual birds in the world calculated using the various methods above, corrected to include seabirds, is summarized in Table 4.

Discussion

The four different methods we applied yield a reasonably consistent estimation of a global total of 200 to 400 billion individual birds ($2-4 \times 10^{11}$); Wood (1982) gives an estimate of 100 billion, but provides no indication of how this was determined. Given the variety of methods, this consistency is gratifying. However, despite the general consistency, there is still some considerable variation in the estimates (in particular in those from Method II), and since the methods are all crude, we would do well first to assess how reliable we believe these estimates to be.

The obvious inconsistency in estimates comes from applying Method II to the data from individual countries, which results in estimates almost an order of magnitude lower than any other method. However, this difference is unsurprising, given that all the countries for which we have data on the number of individual birds are north temperate (Table 2; Osborne and Tigar [1992] classify bird species in Lesotho [30 000 km²] into logarithmic classes of population size, using the midpoint of these classes gives an estimate of 21 760 500 individual birds and a density of 725 km⁻², which is a little higher than those figures in Table 2). Comparison of Tables 1 and 2 shows that the estimates of number of individuals per square kilometre are of similar orders of magnitude in all temperate locations, although the country estimates are still low. Inclusion of data from tropical countries would undoubtedly raise the country estimate considerably. The analyses for Method I indicate that most (around 70%) individual birds are tropical.

There are at least two other general concerns about our estimates. The first is that we have but a single method for estimating seabird numbers, and it is based on the avifauna

Table 4. A summary of the different estimates for the global number of individual birds, including seabirds

Method		Estimate
I	Mean of all local individual densities	3.74×10^{11}
	As above, but excluding data from New Guinea	2.86×10^{11}
	Tropical and temperate regions treated separately	3.51×10^{11}
	As above, but excluding data from New Guinea	2.82×10^{11}
II	Mean estimate from country data	5.33×10^{10}
	Summing country data	8.23×10^{10}
	Mean estimate from continental data	2.06×10^{11}
	Summing continental data	2.30×10^{11}
	Tropical and temperate continents treated separately	2.19×10^{11}
III	Global estimate from regression through the data in II	2.33×10^{11}
IV	Extrapolation from the density–body mass relationship	3.78×10^{11}

of one island. The long coastline of Britain may cause seabird numbers to be overestimated given that many continental areas have no seabirds, but may possibly underestimate them given the apparent abundance of birds in some arctic and antarctic areas. The second is that Method I, and to some extent Method IV, rely on individual bird estimates only from forest sites. If densities of birds in forests differ markedly from the average, then so will the global bird figures.

We think, however, that neither problem is likely to have had a significant effect on the overall magnitude of estimates in Table 4. The estimate for seabirds is far from ideal. Britain is an island, and the percentage of species in its breeding avifauna which comprises seabirds (16%) is quite high; the figure for the global avifauna is around 4% (Sibley and Monroe, 1990). The percentage of individual birds which are seabirds in the British avifauna is thus also likely to be high, suggesting that if anything our estimate of the global number of seabird individuals is likely to be an over estimate. This ignores the possible effect of Antarctica in particular, which contributes significantly to global seabird numbers. However, the percentage of all bird individuals that are seabirds is still likely to remain small.

The regional estimates (Methods II and III) are always lower than those based on local densities (Method I). This could indicate that forest bird densities are on the high side, or result from a general tendency for regional surveys to underestimate bird numbers. We suspect that the former is probably more likely. The reliability of many of the estimates of regional numbers of individuals is difficult to ascertain in any quantitative sense, although the quality of such estimates is improving rapidly, with the detailed analysis of data from spatially extensive census programmes (e.g. Gibbons *et al.*, 1993). The data we used for the number of British landbird individuals (Marchant *et al.*, 1990, as modified by Nee *et al.*, 1991) differ by less than 2% from more recent estimates (Gibbons *et al.*, 1993; we used the earlier data set because of the independent assessment of Nee *et al.* of what subset constituted the native British landbird assemblage).

Estimates based on forest bird densities (essentially from pristine forest sites) are likely to be high because the land area of the planet includes areas such as those turned over to agriculture and habitation, which may house very low bird populations (although some species may attain particularly high densities in such areas). These areas are incorporated in Methods II and III, when estimates for the number of birds in a country are converted into densities using the area of the country. In other words, Method I assumes that all land area is pristine forest bird habitat, which is clearly not the case. However, the estimates from Method I may be close to the number of individual birds the planet could support given no habitat degradation from human causes. About 14% of land has been turned over to agriculture. If we assume that this area now supports no birds (plainly an exaggeration), and that the total that the planet could support is given by the fourth Method I estimate in Table 4 (2.82×10^{11} , which is probably the most realistic figure from Method I), the total number of birds that the planet should now be able to support would be about 2.43×10^{11} birds. This compares favourably with many of the figures obtained using Methods II and III.

Whatever the total number of birds that the planet might be able to support, if we assume that it currently supports 2.5×10^{11} birds, then removing the capability of 1% of land area of the planet to support birds (through habitat destruction, urbanization, etc.) would result in 2500 million individuals losing their habitat. This is probably close to the population size once attained by the passenger pigeon (e.g. see Rosenzweig, 1995, p. 123).

The passing of that species has been much mourned, yet we stand to lose as many birds again and again as the human population continues to expand. This calculation assumes, of course, that birds are uniformly distributed over the planet, which, as we have shown, they are not. Remsen (1995) calculates that, on the basis of minimum estimates of the rate of destruction of tropical forest of 76 000/km² year and a bird density of 1900 km⁻², that the world's population of tropical forest birds is depleted (probably permanently) by 144.4 million individuals per year.

Such figures can be compared with estimated losses to a variety of other sources, although their accuracy is not readily determined: 1000 million migratory birds each year to hunting and trapping in the Mediterranean countries (Magnin, 1991), between 97.6 and 975.6 million birds each year to window strikes in the USA (Klem, 1990), 1.25 million birds to strikes at communication towers and 57.2 million to road kills each year in the USA (Banks, 1979), and 80 million or 319 to 638 million per year to predation by domestic cats in the USA (Winker *et al.*, 1991; Walsberg, 1994). The annual trade in live wild birds is estimated to have been between 2 and 5 million in the 1980s (Thomsen *et al.*, 1992).

If we assume that an estimate of 200 to 300 billion birds is approximately correct, then this amounts to around 40 to 60 individuals per head of the global human population (assuming the human population to be about 5 billion individuals). This strikes us as a remarkably small number, though the ratio of birds to humans is apparently much smaller in some temperate areas of the world (as a result of the increasing density of birds towards low latitudes). For example, in Britain there are approximately 2 to 3 birds per head of human population. Whether global or for smaller scales, such ratios in some sense make the scale of the enterprise of conserving avian biodiversity appear much more tractable. Albeit simplistic, the individual burden of responsibility for this activity is not excessive. Of course, the uneven distribution of birds across the planet places this burden disproportionately on those least able to meet it.

Acknowledgements

K.J.G. is a Royal Society University Research Fellow. T.M.B. was supported by the core grant to the NERC Centre for Population Biology and NERC grant GST/03/1211. John Lawton and an anonymous referee provided helpful comments on the manuscript.

References

- Banks, R.C. (1979) Human related mortality in birds in the United States. U.S. Fish and Wildlife Service Special Scientific Report. Wildlife No. 215.
- Blackburn, T.M. and Gaston, K.J. (1994) The distribution of body sizes of the world's bird species. *Oikos* **70**, 127–30.
- Blackburn, T.M. and Gaston, K.J. (1996) A sideways look at patterns in species richness, or why are there so few species outside the tropics? *Biodiv. Lett.* **3**, 44–53.
- Blackburn, T.M., Gates, S., Lawton, J.H. and Greenwood, J.J.D. (1994) Relations between body size, abundance and taxonomy of birds wintering in Britain and Ireland. *Phil. Trans. R. Soc. Lond. B* **343**, 135–44.
- Brown, L.H., Urban, E.K. and Newman, K. (1982) *The Birds of Africa*, Vol. 1. London: Academic Press.
- Carrascal, L.M. and Tellería, J.L. (1991) Bird size and density: a regional approach. *Am Nat.* **138**, 777–84.

- Cotgreave, P. (1995) Population density, body mass and niche overlap in Australian birds. *Funct. Ecol.* **9**, 285–9.
- Cotgreave, P. and Harvey, P.H. (1994) Phylogeny and the relationship between body size and abundance in bird communities. *Funct. Ecol.* **8**, 219–28.
- Dunning, J.B. (1992) *CRC handbook of Avian Body Masses*. Boca Raton: CRC Press.
- Elton, C. (1927) *Animal Ecology*. London: Sidgwick & Jackson.
- Erwin, T.L. (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopt. Bull.* **36**, 74–5.
- Gaston, K.J. (1991) The magnitude of global insect species richness. *Conserv. Biol.* **5**, 283–96.
- Gaston, K.J. (1992) Regional numbers of insect and plant species. *Funct. Ecol.* **6**, 243–7.
- Gaston, K.J. and Hudson, E. (1994) Regional patterns of diversity and estimates of global insect species richness. *Biodiv. Conserv.* **3**, 493–500.
- Gaston, K.J. and May, R.M. (1992) Taxonomy of taxonomists. *Nature* **356**, 281–2.
- Gibbons, D.W., Reid, J.B. and Chapman, R.A. (1993) *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*. London: T. & A.D. Poyser.
- Groombridge, B. (ed.) (1992) *Global Biodiversity: Status of the Earth's Living Resources*. London: Chapman & Hall.
- Heywood, V.H. (ed.) (1995) *Global Biodiversity Assessment*. Cambridge: Cambridge University Press.
- Hodkinson, I.D. and Casson, D. (1991) A lesser predilection for bugs: Hemiptera (Insecta) diversity in tropical rain forests. *Biol. J. Linn. Soc.* **43**, 101–9.
- Juanes, F. (1986) Population density and body size in birds. *Am. Nat.* **128**, 921–9.
- Klem, Jr. D. (1990) Collisions between birds and windows: mortality and prevention. *J. Field. Ornithol.* **61**, 120–8.
- Kobayashi, S. and Kimura, K. (1994) The number of species occurring in a sample of a biotic community and its connections with species-abundance relationship and spatial distribution. *Ecol. Res.* **9**, 281–94.
- Magnin, G. (1991) Hunting and persecution of migratory birds in the Mediterranean region. In *Conserving Migratory Birds* (T. Salathé, ed.), pp. 63–75. Cambridge: International Council for Bird Preservation.
- Marchant, J.H., Hudson, R., Carter, S.P. and Whittington, P. (1990) *Population Trends in British Breeding Birds*. Tring, Hertfordshire: British Trust for Ornithology.
- May, R.M. (1990) How many species? *Phil. Trans. R. Soc. Lond. B* **330**, 293–304.
- Merikallio, E. (1958) Finnish birds, their distribution and numbers. *Fauna Fennica* **5**, 1–181.
- Nee, S., Read, A.F., Greenwood, J.J.D. and Harvey, P.H. (1991) The relationship between abundance and body size in British birds. *Nature* **351**, 312–13.
- Osborne, P.E. and Tigar, B.J. (1992) Priorities for bird conservation in Lesotho, southern Africa. *Biol. Conserv.* **61**, 159–69.
- Preston, F.W. (1948) The commonness, and rarity, of species. *Ecology* **29**, 254–83.
- Remsen Jr., J.V. (1995) The importance of continued collecting of bird specimens to ornithology and bird conservation. *Bird Conserv. Int.* **5**, 145–80.
- Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.
- Sibley, C.G. and Monroe Jr., B.L. (1990) *Distribution and Taxonomy of Birds of the World*. New Haven: Yale University Press.
- Tellería, J.L. and Carrascal, L.M. (1994) Weight-density relationships between and within bird communities: implications of niche space and vegetation structure. *Am. Nat.* **143**, 1083–92.
- Terborgh, J., Robinson, S.K., Parker III, T.A., Munn, C.A. and Pierpont, N. (1990) Structure and organization of an Amazonian forest bird community. *Ecol. Monogr.* **60**, 213–38.
- Thomsen, J.B., Edwards, S.R. and Mulliken, T.A. (1992) *Perceptions, Conservation and Management of Wild Birds in Trade*. Cambridge: TRAFFIC International.

- Ulfstrand, S. and Hogstedt, G. (1976) Hur manga faglar hackar i Sverige. *Anser* **15**, 1–32.
- Walsberg, G.E. (1994) The use of wild birds in research. *Condor* **96**, 1119–20.
- Williams, C.B. (1960) The range and pattern of insect abundance. *Am. Nat.* **94**, 137–51.
- Wilson, E.O. (1985) The biological diversity crisis. *BioScience* **35**, 700–6.
- Winkler, K., Fall, B.A., Klicka, J.T., Parmelee, D.F. and Tordoff, H.B. (1991) The importance of avian collections and the need for continued collecting. *Loon* **63**, 238–46.
- Wood, G.L. (1982) *The Guinness Book of Animal Facts and Feats*. Enfield, Middlesex: Guinness Superlatives.
- Wright, D.H., Currie, D.J. and Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. In *Species Diversity in Ecological Communities* (R.E. Ricklefs and D. Schluter, eds) pp. 66–74. Chicago: Chicago University Press.