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Source: *Philosophical Transactions: Biological Sciences*, Vol. 351, No. 1342 (Jul. 29, 1996), pp. 897-912

Published by: Royal Society

Stable URL: <https://www.jstor.org/stable/56368>

Accessed: 05-02-2025 20:16 UTC

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# Spatial patterns in the geographic range sizes of bird species in the New World

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## SUMMARY

The attempt to identify and explain pattern in the extent of species' geographical distributions at regional scales has been central to macroecology. However, with the exception of abundance, consistent relations between other variables and species geographic extent have not been forthcoming. One reason may be that studies often encompass the entire geographic ranges of only a fraction of the species in the taxon under consideration, setting biologically artificial boundaries to the area of study, and only revealing part of the pattern in question. Here, we examine patterns in the geographic range sizes of birds in the New World. By testing for patterns in the entire avifauna of a geographically isolated region (95% of species are endemic), we avoid many of the problems of previous studies. Most New World bird species have small geographic ranges, although the frequency distribution of logarithmically transformed ranges is left-skewed. The geographic range size–body size relation is approximately triangular. Small-bodied species may have either large or small ranges, whereas large-bodied species have only large ranges. Species threatened with extinction more often fall nearer to (or below) the lower edge defined by the majority of species in this triangle than do non-threatened species, suggesting that this represents the minimum area needed to sustain viable populations of species of different sizes. The maximum range size attained by species is relatively constant across body sizes, but falls short of the maximum possible given the land area of the New World, and so cannot be limited by this constraint. What does limit maximum range size is thus unclear. There is a latitudinal gradient in the size of species geographic ranges. Species which have the latitudinal mid-point of their geographic ranges at high latitudes either side of the equator tend to have large range sizes, whereas those with mid-points at lower latitudes tend to have small range sizes (as expected from Rapoport's rule). However, this pattern is not symmetrical about the equator, but rather, at about 17° N. It appears to be a consequence of the biogeography of the New World, and implies that mechanisms suggested to explain Rapoport's rule based on climatic variability are incorrect. Migrant birds have larger geographic ranges, on average, than do residents. They are also larger-bodied, and tend to inhabit more northerly latitudes than residents, but their larger ranges are not the simple consequence of these other patterns. The patterns we demonstrate, in particular those relating to maximum range size across body sizes and to latitudinal variation in range size, have significant consequences for the understanding of what determines species geographic range sizes.

## 1. INTRODUCTION

Ecology has been defined as the scientific study of the interactions that determine the distribution and abundance of organisms (Krebs 1972, after Andrewartha 1961). It is small surprise then that a considerable body of biological literature has been devoted to documenting patterns of distribution and abundance, particularly at local scales, as a basis for developing and testing ecological hypotheses (for an overview, see Begon *et al.* 1990). In recent years, evidence has grown that ecological patterns at local and regional scales are not independent, and that the former can often only be understood in the context of the latter (e.g. Ricklefs 1987; Cornell & Lawton 1992; Ricklefs & Schluter 1993). This has led to an upsurge of interest in establishing the form of patterns at the largest scales,

and the emergence of the field of 'macroecology' (Brown & Maurer 1989; Brown 1995). Here, we are concerned with macroecological patterns in the magnitude of one of the two defining variables of ecology: spatial distribution.

### (a) *Macroecological patterns in geographic range size*

When examined over large spatial scales (e.g. a continent), the frequency distribution of geographic range sizes for species in taxonomically constrained assemblages is generally right-skewed (Gaston 1994*a* and references therein); that is, most species have relatively restricted ranges. Most such distributions can be approximately normalized by logarithmic transformation, although frequently the transformed distri-

butions are truncated at larger ranges because of the upper limit to range size imposed by the size of the area of study (e.g. Pagel *et al.* 1991).

Macroecological studies of geographic range size have primarily focused on its interaction with three other variables: body size (e.g. Brown & Maurer 1987, 1989; Sutherland & Baillie 1993; Gaston 1994a; Taylor & Gotelli 1994; Gaston & Blackburn 1996a, b), latitude (Rapoport 1982; Stevens 1989, 1992a; Pagel *et al.* 1991; France 1992; Rohde *et al.* 1993; Letcher & Harvey 1994; Macpherson & Duarte 1994; Roy *et al.* 1994; Ruggiero 1994; Smith *et al.* 1994; Taylor & Gotelli 1994), and abundance (Rabinowitz 1981; Brown 1984; Brown & Maurer 1987; Arita *et al.* 1990; Gaston & Lawton 1990; Hanski *et al.* 1993; Sutherland & Baillie 1993; Gregory & Blackburn 1995). Consensus on how range size is related to the first two of these variables (body size and latitude) has been slow in developing.

The geographic range size–body size relation (one or both variables are often logarithmically transformed) is widely described simply as a positive interaction; large-bodied species tend to have larger geographic ranges than small-bodied. However, examples have been reported in which geographic range size increases with increasing body size, decreases with increasing body size, or follows no simple relation (e.g. Glazier 1980; Reaka 1980; Brown & Maurer 1987, 1989; Gaston 1988, 1994a; Sutherland & Baillie 1993; Cambefort 1994; Inkinen 1994). It now seems clear that much of this variation can be explained in terms of the extent of the geographic coverage of different studies. In general, where significant correlations are found, analyses performed over areas which embrace a very large proportion of the geographic ranges of the species concerned report positive range size–body size relations. In contrast, analyses performed over areas which embrace the entire geographic ranges of none or only a small proportion of the species concerned report positive or negative relations with about equal frequency (Gaston & Blackburn 1996a). Nevertheless, insufficient examples exist unequivocally to establish this rule, and it requires further empirical explanation.

The interspecific relation between the size of a geographic range and its latitudinal position has attained the rarefied status of an ecological ‘rule’ (‘Rapoport’s rule’; Stevens 1989). As first formulated, this states that there is a positive correlation between the latitudinal extent of the geographic ranges (the distance between the northern and southern limits of the range) of species in a taxon, and latitude (Stevens 1989); species with more polar or temperate distributions tend to have larger latitudinal ranges than species with more equatorial or tropical distributions. In this form, and extended to apply to latitudinal variation in geographic range size measured as area (rather than just latitudinal extent), the rule has been shown to hold for a variety of taxa in a variety of regions (Rapoport 1982; Stevens 1989, 1992a; Pagel *et al.* 1991; France 1992; Letcher & Harvey 1994; Ruggiero 1994; Taylor & Gotelli 1994). However, in addition to some documented exceptions (Rohde *et al.* 1993; Macpherson & Duarte 1994; Roy *et al.* 1994;

Smith *et al.* 1994; see also Colwell & Hurtt 1994), the broad generality of the rule remains to be established. First, although it was implicitly formulated to embrace all latitudes, there is no single taxon for which this has been demonstrated. The best evidence comes from comparison of latitudinal patterns in North and South American mammals (Pagel *et al.* 1991; Ruggiero 1994). However, results from the South American fauna are equivocal in demonstrating Rapoport’s rule (Ruggiero 1994), suggesting that the pattern observed may depend on the particular taxon of mammals concerned. Further, the comparison of results for the two continents is not strictly valid, because the ranges of species found on both continents are not truly represented.

The second weakness, related to the first, is that most studies have dealt with northern hemisphere faunas. Those that have considered faunas within the southern hemisphere have provided only equivocal support for Rapoport’s rule (Rohde *et al.* 1993; Macpherson & Duarte 1994; Ruggiero 1994; Smith *et al.* 1994).

Third, random sampling models and the effects of ‘hard boundaries’ (e.g. northern and southern edges to land masses) on range limits (Colwell & Hurtt 1994) suggest mechanisms that may generate spurious latitudinal gradients in range sizes. If geographic ranges are randomly distributed across a land mass, but species in the north and south have ranges truncated by the land’s end, a negative latitudinal gradient in range sizes (the opposite of Rapoport’s rule) can result. Alternatively, a negative latitudinal gradient in species richness (as generally observed) can generate a spurious Rapoport effect given constant sampling effort, because species in areas of high richness are relatively undersampled. Although these mechanisms are likely to be of less concern for well-known taxa, they may well explain patterns in more poorly known groups.

#### (b) *Range size patterns in New World birds*

Given current understanding of relations between geographic range size and body size, and between geographic range size and latitude, it would be useful to explore them using an assemblage that allows some of these uncertainties to be addressed, and simultaneously circumvents at least some of the analytical problems. Testing multiple patterns in the same assemblage has the additional advantage that it allows the interrelation between them to be examined. In this paper, we examine patterns in the geographic range sizes of the assemblage of birds of the New World. This assemblage has a number of features that make it particularly suitable for such a study.

1. The New World is a relatively discrete land mass, generally isolated from other land areas. As a result, a high proportion of its fauna (95% of the birds) is endemic to the region. Problems resulting from the geographic ranges of species extending beyond the bounds of the region (e.g. as in the interaction between range size and body size) can thus be greatly reduced.

2. The New World extends across a wide range of latitudes, allowing latitudinal patterns to be plotted that span the equator and two temperate regions.

3. Bird distributions through most of the New World are very well known (at least at the resolution with which we are concerned). This minimizes the potential for the production of spurious latitudinal gradients. Distribution maps are available for all extant New World bird species, meaning that the potential for bias to be introduced through missing species is also minimized (see Blackburn & Gaston (1994*a, b*) for examples of how missing species can affect a macroecological pattern). This potential is not entirely eradicated, because some bird species may as yet be undiscovered (Blackburn & Gaston 1994*b*, Gaston & Blackburn 1994); however, such species will be a small proportion of the total currently known.

4. The New World avifauna is the most speciose of any region. Therefore, not only is the taxon well-known, but it also gives a good sample size for detecting possible patterns.

5. The phylogeny of the birds is reasonably well-known. Any analysis of patterns across large numbers of related species should include consideration of how common ancestry might affect the relations observed (Harvey & Pagel 1991). All the geographic range size relations discussed above may result from the effects of phylogenetic relatedness among the taxa analysed. For example, positive range size–body size interactions in birds may arise because of differences between passerines and other bird taxa. The former are small-bodied, have recently radiated (Sibley & Ahlquist 1990; Nee *et al.* 1992), and so may have smaller geographic ranges than other, generally larger-bodied bird taxa.

Specifically, we address the following questions in this paper: How are the geographic range sizes of New World birds distributed? What is the relation between geographic range size and body size in these data? Is there evidence for latitudinal patterns in geographic range size? How does migratory status interact with any observed patterns? How do phylogenetic relations affect any observed patterns?

## 2. METHODS

### (a) *The assemblage*

For present purposes, the New World was defined as continental North, Central and South America, the Caribbean, and islands close to the continental landmass (e.g. the Aleutians to 170° W, Cocos Island, Isla Guadalupe). Islands further offshore, and in the Antarctic region, were excluded (e.g. the Revillagigedos, Galapagos, Juan Fernandez and Falkland Islands, South Georgia and Bermuda). A working list for the region of 3 906 bird species was arrived at, which included land and seabirds, but excluded introduced species (e.g. *Sturnus vulgaris* L.). For taxonomic consistency, we generally followed the species list and classification of Sibley & Monroe (1990, with emendations following Sibley & Monroe 1993), with the exception of a few species listed in this work but considered definitely extinct (e.g. *Ara cubensis* Wetherbee, *Siphonorhis americana* L.), and a few species discovered since its publication (mainly dealt with by Ridgely & Tudor 1994).

### (b) *Range size data*

Information on the geographic distributions of bird species were obtained from the following sources: Delacour & Amadon (1973); de Schauensee & Phelps (1978); Forshaw (1981); Goodwin (1983); Bond (1985); Harrison (1985); Hayman *et al.* (1986); Hilty & Brown (1986); Dunning (1987); National Geographic Society (1987); Madge & Burn (1989, 1993); Ridgely & Gwynne (1989); Ridgely & Tudor (1989, 1994); Stiles & Skutch (1989); Turner & Rose (1989); Fjeldså & Krabbe (1990); Burton (1992); del Hoyo, Elliott & Sargatal (1992, 1994); Fry *et al.* (1992); Clement *et al.* (1993); Curson *et al.* (1994); Howell & Webb (1995). Most of these works have been published in the last 10 years, so for most species we can have confidence that our information is relatively recent. Any bias introduced by older information will (sadly) tend to lead to the overestimation of species' present geographic range sizes. Because all range sizes are anyway likely to be overestimated by our methodology (see below), this is unlikely to be a significant problem. The data contained in these sources is of variable quality. We preferentially used those sources with the most precisely delineated range maps (e.g. Fjeldså & Krabbe 1990; Ridgely & Tudor 1989, 1994; Howell & Webb 1995), and cross-checked sources where possible.

Each species' distribution was transcribed onto a cylindrical equal area (e.g. Peter's) projection map of the New World, overlaid by the WORLDMAP equal area grid for the region. This grid is a cylindrical projection of the world divided into equal-area squares for intervals of 10° longitude (each approximately 611 000 km<sup>2</sup>; Williams 1992, 1993), and symmetrical about the equator. The region of interest here falls within 116 of these squares, which contained varying areas of land. We calculated the proportion of land area in each square by overlaying the Peters projection map with a grid of 121 (11 × 11) regularly spaced dots, and counting the number that fell entirely or partly on land. A species' total geographic range size (hereafter called 'total range size' to distinguish it from the generic use of 'geographic range size') was taken to be the number of grid squares into which its range extended, multiplied by the proportion of land area in those squares. The largest possible total range size using this method, obtained if a species is found in at least part of all 116 grid squares, is 68.55 units. Each species' breeding range was calculated in the same way, using only those grid squares in which a species was recorded as breeding. Populations known to have been the result of human introduction were not used for either measure. Both measures are likely to be overestimates (see Smith *et al.* 1994); the direction of bias will be consistent across all species. In the terminology of Gaston (1991, 1994*b*), these range size measures are of areas of occupancy, albeit very crude ones.

The spatial scale at which our analysis is performed has been used to investigate a variety of patterns in biodiversity and macroecology (e.g. Eggleton 1994; Eggleton *et al.* 1994; Williams *et al.* 1994; Williams & Humphries 1996; Gaston *et al.* 1995; Gaston &

Williams 1996; Gaston & Blackburn 1996*c*). Although undoubtedly crude, it offers a useful compromise between a resolution that is fine enough to detect real biological variation, and one that is so fine that it detects variation in sampling and knowledge. In fact, geographic ranges tend to be correlated across different scales of analysis (Gaston 1994*a*), so that species that have large geographic range sizes measured over large scales also have large ranges measured over small scales. For example, there is a strong positive relation between the range sizes we calculate for a set of birds of the eastern Andes, and the ranges calculated by Graves (1985) for the same species just within Peru (Spearman rank correlation,  $\rho = 0.683$ ,  $n = 262$ ,  $p < 0.0001$ , excluding those ranges Graves calculated for superspecies). Experience suggests that broad scale geographic patterns are detectable using the scale we do, and throughout our analyses of the New World birds no relevant previously known patterns of variation in species richness, body size and other variables have failed to emerge (Gaston & Blackburn 1996*c*; Blackburn & Gaston 1996*a, b*).

### (c) *Latitudinal distributions*

The distribution data were used to calculate estimates of the latitudinal position of each species' breeding range. In analyses of latitudinal patterns, all latitudes in the northern hemisphere were arbitrarily assigned negative values. The latitudinal mid-point of the breeding range was calculated as  $(L_s + L_N)/2$ , where  $L_N$  is the latitude of the northern boundary of the northernmost square, and  $L_s$  the latitude of the southern boundary of the southernmost square in which the species bred. For all analyses of latitudinal patterns, species' breeding range size was used in preference to the latitudinal extent of a species' total range. Colwell & Hurr (1994) discuss some of the problems associated with the use of latitudinal extents. Using breeding range avoided complications introduced by species with disjunct breeding and wintering ranges in which the latitudinal mid-point can fall at a latitude at which the species does not occur. Species with disjunct breeding areas can still produce this situation, but it is much less common.

Latitudinal patterns in breeding range sizes were analysed using four different methods.

#### (i) *Across-species method*

We examined latitudinal patterns across species, using all species as separate data points in the analysis.

#### (ii) *Stevens' method*

We tested for latitudinal variation in the mean breeding range size of all species whose ranges cross a line of latitude (Stevens 1989), using the mid-point of each latitudinal row in the WORLDMAP grid as a line of latitude. This method has frequently been used to examine latitudinal gradients in range size (Stevens 1989, 1992*a*; Pagel *et al.* 1991; France 1992; Letcher & Harvey 1994; Ruggiero 1994), but suffers from several problems (see Pagel *et al.* 1991; Rohde *et al.* 1993; Colwell & Hurr 1994; Letcher & Harvey 1994). Not

least of these is that a single species can contribute to the mean breeding range at more than one latitude, so that latitudinal means are not statistically independent. We use this method here because it is unique in incorporating information on the range sizes of all species occurring at each latitude; other methods show only the mean range size of those species whose ranges are centred on a latitude.

#### (iii) *Mid-point method*

For each row of squares on the WORLDMAP grid (the New World is spanned by 22 such rows), we calculated the geometric mean breeding range size for all species whose latitudinal mid-points fell within the latitudinal limits of that row. This method is similar to Stevens' method, but differs in that each species is used only once in calculating the means, and values for neighbouring rows are therefore independent (Rohde *et al.* 1993).

#### (iv) *Comparative method*

We repeated the analyses of the across-species method, but controlling for the non-independence of data points resulting from the phylogenetic relatedness of species, using a phylogenetic comparative method (see Harvey & Pagel 1991). One way to control for the effects of phylogenetic relatedness is to examine relations within each pair of taxa below a node in a bifurcating phylogeny. The relation between the variables is then unaffected by phylogeny, because the taxa in each comparison are equally related to each other. This method requires that the true phylogeny be known (Felsenstein 1985). Here, we use a model (evolutionary covariance method; Pagel & Harvey 1989; Harvey & Pagel 1991) which applies Felsenstein's approach to datasets for which only approximate phylogenies are available. This method calculates a single value ('contrast') for each variable within each taxon (for species within each genus, genera within each tribe, etc), which represents the magnitude and direction of the change in the variable within the taxon. Each contrast is then scaled using an assumption about branch lengths in the phylogeny (Pagel & Harvey 1989; Harvey & Pagel 1991). The independent contrasts calculated for two variables will show similar changes within each taxon if they are correlated. The set of within-taxon contrasts can then be analysed using standard regression techniques (Pagel & Harvey 1989; Harvey & Pagel 1991), although regressions on contrasts must be forced through the origin (Garland *et al.* 1992).

The evolutionary covariance method was implemented using a program written by M. D. Pagel (a more recent program for applying this approach (Purvis & Rambaut 1995) could not be used here, because our dataset was too large to be encoded in the form required), on the phylogeny of Sibley & Ahlquist (1990), with classification below the level of tribes based on Sibley & Monroe (1990, 1993). We used this phylogeny while aware of the criticisms (e.g. Houde 1987; Sarich *et al.* 1989; Harshman 1994; but see Mooers & Cotgreave 1994); despite the potential



biases and subjectivity, it is currently probably the best, and certainly the most extensive, avian phylogeny available.

We additionally calculated the latitudinal mid-point of each row on the WORLDMAP grid, and the total amount of land area available to species whose mid-points fall in that row: that is, the amount of land within the limits encompassed by the largest possible latitudinal extent that a species can have, given the row in which its latitudinal mid-point falls.

Any test for latitudinal patterns in species range sizes faces at least three analytical problems that must be addressed before meaningful conclusions can be drawn from observations. First, latitudinal patterns in range size may reflect patterns in land shape, rather than anything biological. Hence, latitudinal variation in the land area available to species must be taken into account. Second, neither the latitudinal extent nor the absolute size of a species' range is independent of the latitude at which its range mid-point falls (Colwell & Hurtt 1994). Species with high latitude mid-points are constrained to have smaller latitudinal extents, and cannot attain range sizes that are as large as those attained by species with low latitude mid-points. On this basis alone, both the mean and variance in range size would be expected to decrease as the distance of the latitudinal mid-point from the equator increases. One way to circumvent these two problems is to examine range sizes in relation to the amount of land area available to species at a given latitude, or with range mid-points in a given latitudinal row. Specifically, we ask whether there is latitudinal variation in the proportion of the land area available to a species that the species actually occupies.

Third, and related to the second point, there will be boundary effects in species ranges at the latitudinal extremes of the geographic region. In most cases, it will be impossible to say whether species whose ranges abut the northern or southern limits of a land mass are at their biological limits, or whether their ranges are simply curtailed by land's end (point one is the east-west analogue of this). This effect is likely to be particularly strong at the southern tip of South America, which lies almost 20° further from the Pole than does the northernmost point in North America, and will tend to reinforce the apparent reduction in range size at high latitudes caused by the second point above. To remove this effect, all analyses of latitudinal patterns excluded those 285 species whose ranges included either the northernmost or southernmost latitudinal row (referred to as 'latitudinally restricted' species; all other species are 'latitudinally unrestricted').

In addition to these standard analytical problems, using the WORLDMAP grid to map the geographic distributions of species introduces a small bias into the calculation of latitudinal mid-points. Each successive grid row away from the equator covers a greater latitudinal extent, so that rows either side of the equator cover 5° of latitude, whereas the most northerly row containing latitudinally unrestricted species covers 12°. This means that species' latitudinal mid-points will appear to be nearer the Pole than if squares of

equal latitudinal extent were used. The effect will be greater on average for species with broader latitudinal ranges, and less for species with ranges spanning the equator, where the effect is partly or completely cancelled. Overall, the bias may increase the chance of observing a Rapoport effect, because species with large latitudinal ranges but present in only one hemisphere should be most affected. However, note that the bias can move a calculated latitudinal mid-point less than 6° at most, and then only for mid-points of 30° N and over. Thus, it can only move a mid-point into the row of the grid adjacent to that in which it would have fallen were there no bias.

#### (d) *Body size and status*

In addition to data on geographic distributions, we collated information on the **biology and rarity status of bird species** occurring in the New World. Analyses involving these variables were performed both across species, using the method of **ordinary least squares for all regression analyses**, and within taxa, using the evolutionary covariance method (described above) to control for phylogenetic effects.

Body masses (grammes) for 2913 of the 3906 species were taken from Dunning (1992), and Gaston & Blackburn (1994). Where possible, estimates of female mass were used, but otherwise we used whatever species masses were available. If a range of masses was given instead of a mean mass, we used the arithmetic mean of the limits. **All masses were  $\log_{10}$  transformed for analysis** (Harvey 1982).

Species were classified according to whether they were New World endemics or not, seabirds or landbirds, and migrant or resident. A species was considered to be a New World endemic if its breeding range was entirely restricted to the New World area as previously defined (3 692 species). Species were classified as seabirds if their feeding and/or wintering ranges were pelagic (e.g. all Procellariiformes, Sulidae, Fregatidae, Phaethontidae, and Alcidae, and some Stercoracidae, Laridae, and Sternidae; 76 species in total). Seabirds generally use land only for nesting, and so their geographic range sizes are likely to be seriously underestimated in our analyses; hence they were excluded from some analyses. The migratory status of species was defined by the coincidence of their breeding and total ranges. A species was classified as resident if the two measures were totally coincident, and migrant if they were not (i.e. if its total range was larger than its breeding range).

Species were classified in terms of the threat of extinction they presently face, depending on whether or not they were included in BirdLife International's world list of threatened birds (Collar *et al.* 1994); all species not on this list were considered to be non-threatened, unless there was reason to believe that they had been left off the list because they were considered already extinct. Collar *et al.* further classified threatened species into classes according to the degree of threat which they are considered to face (in decreasing order of threat, these classes are extinct, extinct in the wild, critical, endangered, and vulnerable), and ad-

ditionally list species whose survival they consider conservation dependent, species for which data are inadequate for accurate threat assessment, and species that they consider near-threatened. We classified threatened species following the same system, but note that none of the species considered conservation dependent are found in the New World as defined here.

3. RESULTS

(a) *Distribution of range size*

The frequency distributions of both the total and breeding range sizes of New World birds are strongly right-skewed (figure 1). Logarithmic transformation approximately normalizes these distributions (figure 2), but both actually become significantly left-skewed ( $\log_{10}$  total range,  $t = -14$ ,  $p < 0.001$ ,  $n = 3906$ ;  $\log_{10}$  breeding range,  $t = -15$ ,  $p < 0.001$ ,  $n = 3901$ ; with skewness measured as  $g_1$ , and using the significance test in Sokal & Rohlf 1981). Restricting analysis to endemic landbirds does not alter these results (table 1). Similarly, there is little difference between the range

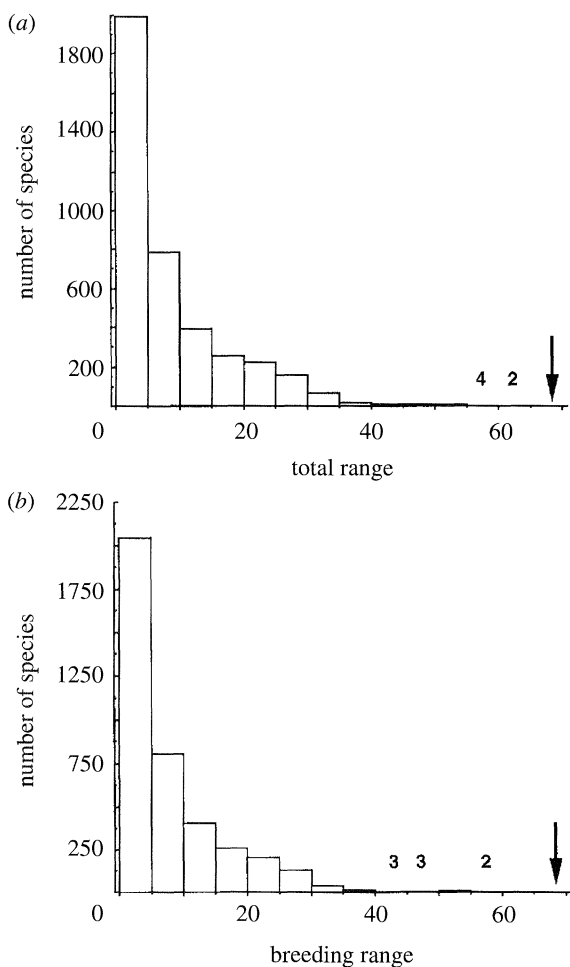


Figure 1. The frequency distribution of (a) geographic range and (b) breeding range for New World birds. Numbers above some columns indicate the number of species in that range size class. See text for the method (and units) used to measure range size. The maximum possible range size in these units is 68.55 (arrowed).

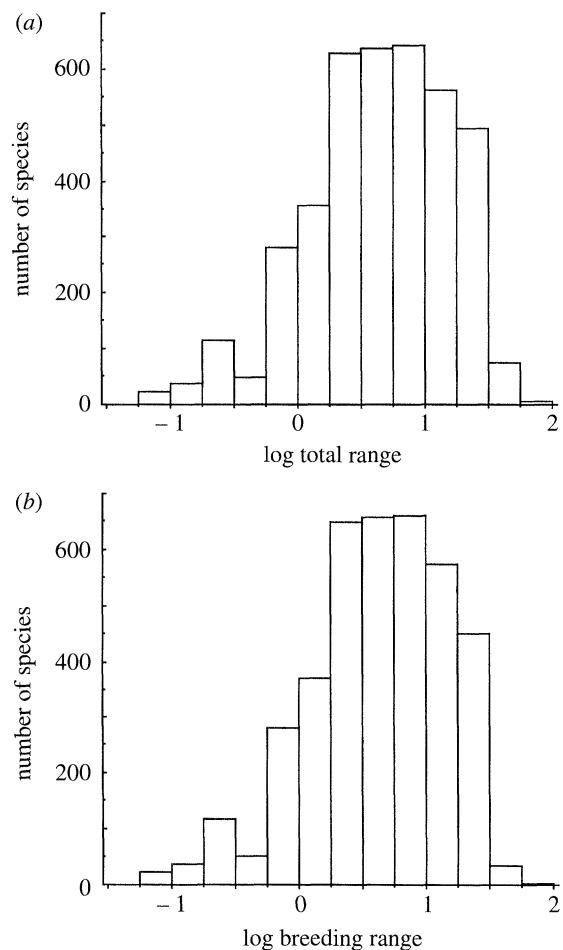


Figure 2. As figure 1, but displayed as the frequency distribution of (a)  $\log_{10}$  total range and (b)  $\log_{10}$  breeding range for New World birds. The  $\log_{10}$  maximum possible range size is 1.836.

size distributions of passerine and non-passerine birds, although the range sizes of passerines are consistently slightly smaller (table 1).

Because of the high skewness of the untransformed variable, we have used  $\log_{10}$  transformed range size in all subsequent analyses. Although a square root transformation is perhaps more logical for area variables,  $\log_{10}$  transformation allows our results to be directly compared with previous interspecific analyses of range size (see Introduction and e.g. Brown & Maurer 1987, 1989; Gaston & Blackburn 1996*a, b*).

(b) *Relations between range size and body mass*

The relation between breeding range size and body mass for all species of bird in the New World is shown in figure 3 (for the sake of simplification, we only present results for breeding range size here; those for total range are both qualitatively and quantitatively similar). There is an extremely weak, albeit highly statistically significant, positive correlation but the data are better described by a triangular than a linear relation. The upper and left-hand boundaries of this triangle are relatively well defined, but the hypotenuse is much less so. However, if analysis is restricted to endemic landbirds considered by Collar *et al.* (1994)

Table 1. Statistics for the frequency distributions of logarithmically transformed measures of range size (Var = variance,  $g_1$  = skewness (Sokal & Rohlf 1981),  $n$  = number of species.)

	log <sub>10</sub> total range				log <sub>10</sub> breeding range			
	mean	var.	$g_1$	$n$	mean	var.	$g_1$	$n$
all species	0.64	0.31	−0.55	3906	0.62	0.29	−0.59	3901
passerines	0.62	0.28	−0.54	2266	0.60	0.27	−0.58	2295
non-passerines	0.67	0.34	−0.58	1640	0.64	0.33	−0.61	1636
endemic landbirds	0.64	0.29	−0.55	3677	0.62	0.28	−0.57	3676
passerines	0.62	0.28	−0.56	2242	0.60	0.27	−0.58	2241
non-passerines	0.66	0.31	−0.56	1435	0.64	0.30	−0.58	1435

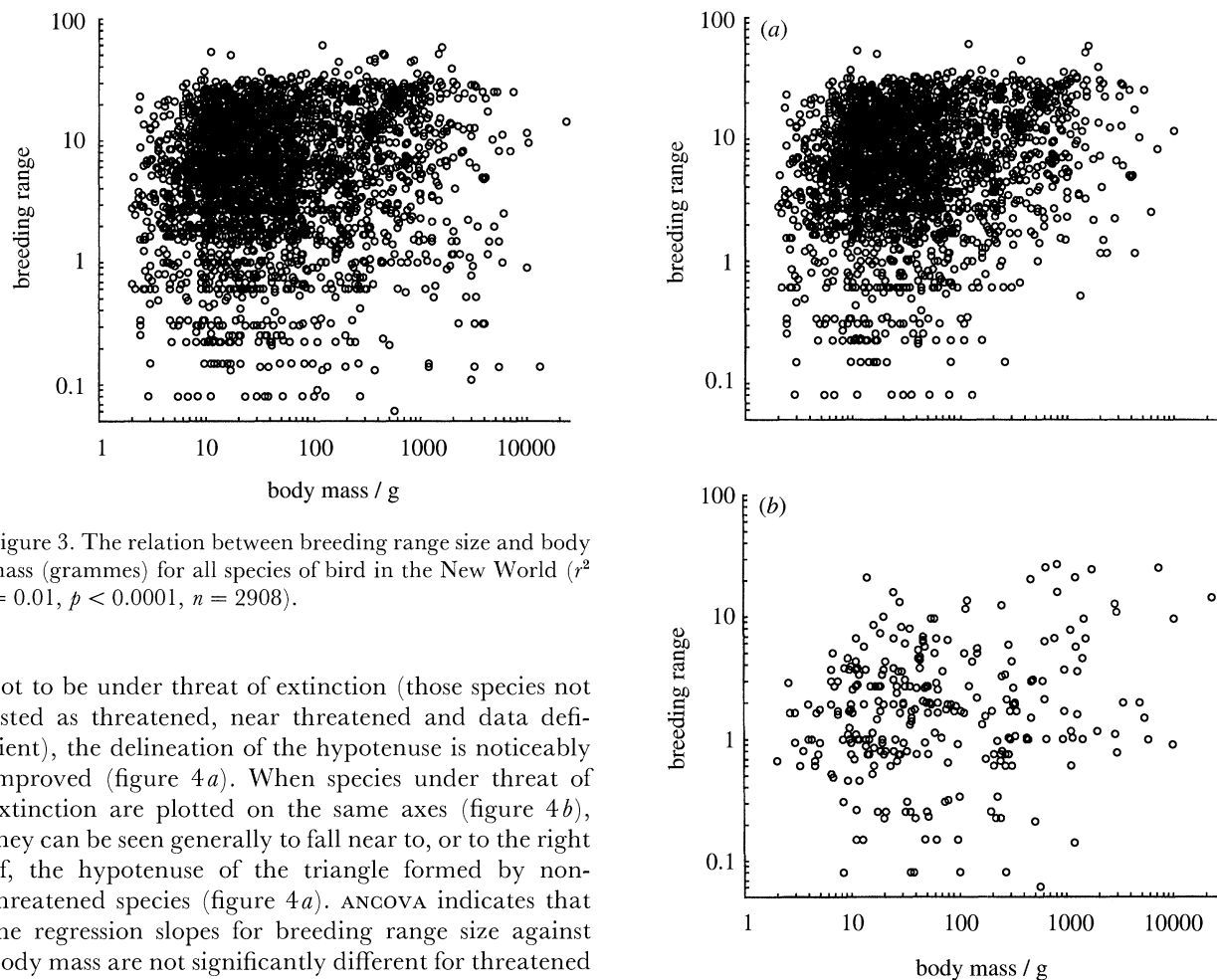


Figure 3. The relation between breeding range size and body mass (grammes) for all species of bird in the New World ( $r^2 = 0.01$ ,  $p < 0.0001$ ,  $n = 2908$ ).

not to be under threat of extinction (those species not listed as threatened, near threatened and data deficient), the delineation of the hypotenuse is noticeably improved (figure 4a). When species under threat of extinction are plotted on the same axes (figure 4b), they can be seen generally to fall near to, or to the right of, the hypotenuse of the triangle formed by non-threatened species (figure 4a). ANCOVA indicates that the regression slopes for breeding range size against body mass are not significantly different for threatened and non-threatened species ( $F_{1,2904} = 0.39$ ,  $p = 0.5$ ), but that their elevations do differ significantly ( $F_{1,2905} = 384$ ,  $p < 0.0001$ ).

Within taxa, there is no significant relation between body mass and either total range size or breeding range size, both when all species or just endemic landbirds are included in analyses (table 2). Because the relation between range size and body mass is positive but triangular (and hence not strictly linear) across species, we might expect to see the same pattern within taxa. If so, we would expect positive contrasts between range size and body mass to predominate within taxa, even if there is no simple relation across contrasts. However, there is no tendency for a predominance of positive within-taxon contrasts between range size and body mass in these data (table 2), suggesting that there is no consistent relation within taxa.

Figure 4. The relation between breeding range size and body mass (grammes) for (a) New World endemic landbird species not listed as under threat of extinction ( $r^2 = 0.035$ ,  $p < 0.0001$ ,  $n = 2423$ ), and (b) New World endemic species listed as under threat of extinction (species listed as threatened, near threatened and data deficient) by Collar *et al.* (1994) ( $r^2 = 0.03$ ,  $p = 0.003$ ,  $n = 281$ ).

(c) Relations between breeding range size and latitude

Analyses of relations between range size and latitude were restricted to latitudinally unrestricted, New World endemic landbird species, a maximum of 3 521 species.

Using the across-species method, maximum breeding range size appears to reach a minimum at between



20° N and 10° N, and to increase both to the north and to the south of these latitudes (figure 5*a*). However, maximum breeding range size in the southern hemisphere does not seem to be attained at the highest latitudes, but rather just south of the equator. Thus, although both linear and squared terms of a second order polynomial fitted to the data in figure 5*a* explain significant (albeit small) amounts of the variation in range size (overall  $r^2 = 0.045$ ,  $p < 0.0001$  for both regression terms), additionally introducing a cubic term to the regression causes a marked increase in the amount of explained variation (overall  $r^2 = 0.18$ ,  $p < 0.0001$  for each of the three regression terms). This increase reflects the decrease in mean geographic range size south of the equator.

The decrease in breeding range size with latitude south of the equator must be due in part to the decreasing land area available for species at these latitudes. By excluding latitudinally restricted species, this effect is reduced, but not entirely obviated. To control for differences in land area with latitude, we plotted latitude against the proportion of the total land area available to a species that it actually occupies (figure 5*b*). Species at latitudes either side of about 17° N on average occupy greater proportions of the available area than do species at around this latitude. Range size does not decrease so markedly with latitude south of the equator. Nevertheless, a third order polynomial regression fitted to the data in figure 5*b* still explains much more of the variation in range size than does a second order (third order  $r^2 = 0.30$ , second order  $r^2 = 0.17$ ,  $p < 0.0001$ ,  $n = 3520$  in both cases), indicating that there is still a tendency for range size to decline at latitudes greater than about 20° S.

The mid-point method reveals similar patterns to the across-species method. This is not surprising, because effectively it expresses the mean trend demonstrated by the previous method. Thus breeding range size again reaches a minimum at between 20° N and 10° N, but with maximum breeding range size in the southern hemisphere attained just south of the equator, rather than at the highest latitudes (figure 6*a*). If latitude is plotted against the mean proportion of the

Table 2. *Within-taxon relations between log<sub>10</sub> body mass (in grammes) and the log<sub>10</sub> transformed variable in the first column, calculated using the evolutionary covariance method (Pagel & Harvey 1989; Harvey & Pagel 1991)*

( $n$  = number of independent contrasts (see Methods),  $p$  = probability that the correlation between range size and body size does not differ from zero. Positive = the number of taxa (out of the total  $n$ ) for which the independent contrast of body mass on the variable in the first column was positive. There are no more or less positive contrasts than expected by chance alone: two-tailed binomial  $p > 0.05$  in all cases.)

	$r^2$	$n$	$p$	positive
all species				
total range size	0.0001	625	0.82	294
breeding range size	0.0001	624	0.76	295
endemic landbirds				
total range size	0.001	564	0.48	262
breeding range size	0.001	564	0.41	263

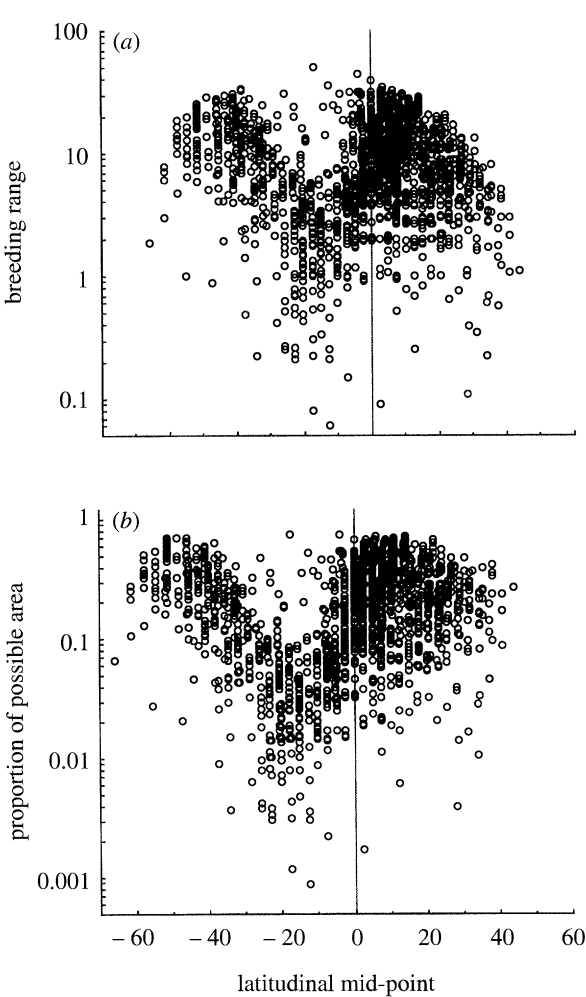


Figure 5. The across-species relation between the latitudinal mid-point of a species breeding range and (a) its breeding range size; (b) the proportion of the total land area available to a species that the species actually occupies (see text). The equator is indicated by a vertical line; negative latitudes are in the northern hemisphere. Only latitudinally unrestricted (see text), New World endemic landbirds are included.

total land area available to a species in a row that the species actually occupies (figure 6*b*), the proportion occupied also reaches its minimum between 20° N and 10° N. However, south of the equator there is no tendency for this proportion either to decrease or to increase with latitude (figure 6*b*).

Stevens' method reveals qualitatively some of the main features of the previous two methods, but the patterns are more clear cut (figure 7), as would be expected given the degree of autocorrelation (through shared species) inherent in the method. Thus, the smallest average breeding range is still attained at between 20° N and 10° N (figure 7*a*), but now the pattern to the south of this point more closely mirrors that to the north. This is much more marked when continental shape is controlled for by comparing, across latitudes, the mean proportion of the area available to a species with a given latitudinal mid-point (figure 7*b*): species at high latitudes have larger breeding ranges, and utilize a higher proportion of the area available to them, than do species at lower latitudes.

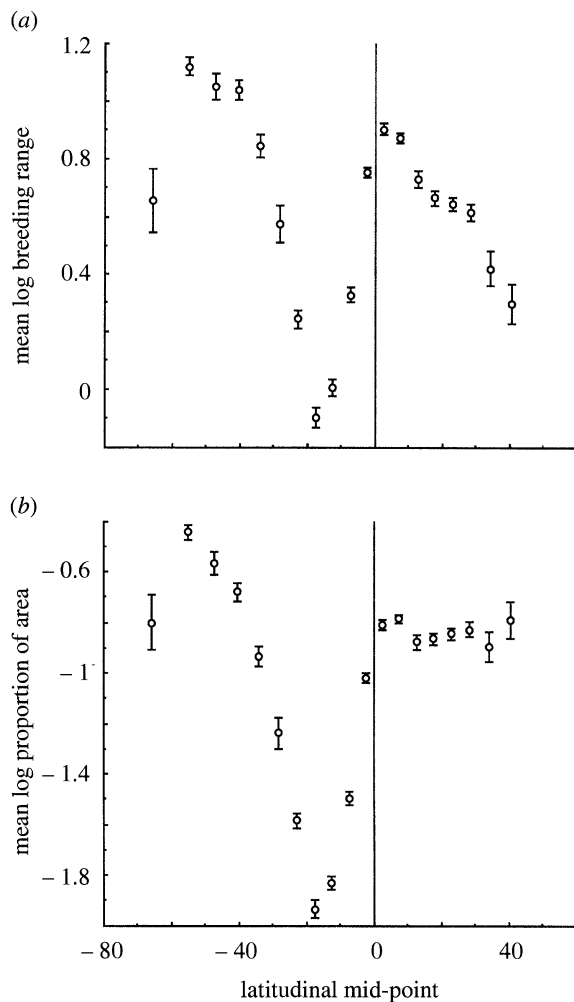


Figure 6. The relation between the latitudinal mid-point of a row on the WORLDMAP grid and (a) the mean ( $\pm$ s.e.)  $\log_{10}$  breeding range size of species with latitudinal mid-points in that row (mid-point method); (b) the mean ( $\pm$ s.e.)  $\log_{10}$  proportion of the total land area available to a species with its latitudinal mid-point in that row that the species actually occupies. The equator is indicated by a vertical line; negative latitudes are in the northern hemisphere. Only latitudinally unrestricted (see text), New World endemic landbirds are included.

The comparative method shows that, within taxa, there is a weak tendency for breeding range size to increase with absolute latitudinal distance from the equator ( $r^2 = 0.035$ ,  $p < 0.0001$ ,  $n = 624$ ). However, this result is clearly affected by non-linearity in the latitudinal patterns across species. Range sizes increase both north and south of about  $17^\circ$  N, but the comparative method can only detect unidirectional relations (i.e. it can determine whether a relation is positive or negative, but not whether parts of the relation show different trends). To circumvent this problem, we assumed that breeding range size reaches its minimum at  $17^\circ$  N in New World birds, and calculated the absolute latitudinal distance of each species' latitudinal mid-point from this minimum (species with latitudinal mid-points at  $37^\circ$  N and  $3^\circ$  S both have the same absolute latitudinal mid-point about  $17^\circ$  N). Within taxa, there is a positive relation between this value and breeding range size ( $r^2 = 0.23$ ,

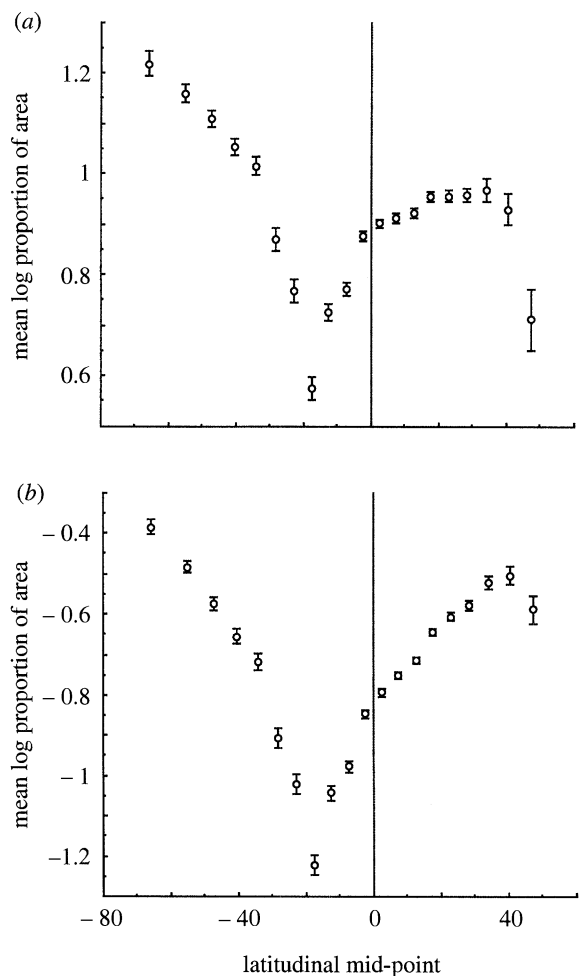


Figure 7. The relation between the latitudinal mid-point of a row on the WORLDMAP grid and (a) the mean ( $\pm$ s.e.)  $\log_{10}$  breeding range size of all species whose ranges include that row (Stevens' method); (b) the mean ( $\pm$ s.e.)  $\log_{10}$  proportion of the total land area available to a species that the species actually occupies, calculated using all species whose ranges include the row. The equator is indicated by a vertical line; negative latitudes are in the northern hemisphere. Only latitudinally unrestricted (see text), New World endemic landbirds are included.

$p < 0.0001$ ,  $n = 624$ ): for a sub-taxon within a taxon, on average, the further is its latitudinal mid-point from  $17^\circ$  N, the larger is its breeding range. The same is also true if breeding range is substituted by the ( $\log_{10}$ ) proportion of area available that is actually used ( $r^2 = 0.49$ ,  $p < 0.0001$ ,  $n = 624$ ).

#### (d) Relations between range size and migratory status

Migrant New World birds have, on average, larger breeding range sizes than resident species (mean  $\log_{10}$  breeding range size of migrants = 0.96, of residents = 0.57; ANOVA,  $F_{1,3899} = 221$ ,  $p < 0.0001$ ). The result holds if analysis is restricted to endemic landbirds (migrants = 0.93, residents = 0.58; ANOVA,  $F_{1,3674} = 157$ ,  $p < 0.0001$ ). Migrants are also on average larger-bodied than residents (all species: mean  $\log_{10}$  body mass of migrants = 1.90, of residents = 1.60, ANOVA,  $F_{1,2906} = 69.7$ ,  $p < 0.0001$ ; endemic landbirds: mi-

grants = 1.73, residents = 1.55, ANOVA,  $F_{1,2697} = 21.2$ ,  $p < 0.0001$ ). The relation between breeding range size and migratory status may therefore arise because migrants are larger-bodied, and larger-bodied species on average have larger breeding ranges (figures 3, 4). Unfortunately, we cannot use ANCOVA to test for a relation between range size and migratory status independent of body mass, because the assumption of homogeneity of slopes is violated by the data (all species,  $F_{1,2904} = 7.8$ ,  $p = 0.005$ ; endemic landbirds,  $F_{1,2695} = 19.3$ ,  $p < 0.0001$ ). However, the relation of migratory status to breeding range size seems stronger than to body mass, and we suspect that, if anything, the body mass-migratory status relation is likely to result from the range size-migratory status relation, rather than vice versa.

Some evidence for this point of view is provided by comparative analysis. Within taxa, migrants have larger breeding ranges than residents more often than expected by chance alone, whether all species are analysed (migrants have larger ranges in 156/225 taxa, two-tailed binomial  $p < 0.0001$ ) or if analysis is restricted to endemic landbirds (131/200 taxa,  $p < 0.0001$ ). However, migrants show no tendency to be larger-bodied than residents within taxa (all species: migrants are larger-bodied in 91/183 taxa,  $p = 0.99$ ; endemic landbirds: 103/206 taxa,  $p = 0.94$ ).

Migrants and residents are not distributed randomly with respect to latitude. Rather, migrants have

breeding ranges with significantly more northerly latitudinal mid-points (mean mid-point for migrants =  $26.7^{\circ}$  N, for residents =  $0.7^{\circ}$  S; ANOVA,  $F_{1,3899} = 725$ ,  $p < 0.0001$ ). The relation between range size and migratory status could be an artefact of the latitudinal gradient in range size, which is best defined in the north (figures 5–7), the region containing the most migrant species. This does indeed seem to be partly the case. A significant difference between the breeding range sizes of migrants and residents was found within only 5 of the 18 rows of the WORLDMAP grid in which the comparison could be made (table 3). However, one reason for the failure to find more significant differences is that many latitudinal bands encompass the mid-points of the breeding ranges of only a handful of migrant species: migrants have larger breeding ranges than residents in 17 of the 18 grid rows (binomial  $p = 0.0003$ ). Within taxa, migratory status explains a significant, though small, amount of the variation in  $\log_{10}$  breeding range unexplained by absolute latitudinal distance from  $17^{\circ}$  N, when the independent contrasts on all three variables are analysed simultaneously using multiple regression (partial  $r = 0.12$ ,  $p = 0.009$ ,  $n = 498$ : migrants have larger range sizes).

Resident species are also more likely to be considered threatened (including near threatened) than are migrants ( $\chi^2 = 43.4$ ,  $p < 0.0001$ , d.f. = 1), and the same is true if just endemic landbirds are analysed ( $\chi^2 = 28.5$ ,  $p < 0.0001$ , d.f. = 1), or if threat classes are included separately in the analysis (for endemic landbirds,  $\chi^2 = 28.8$ ,  $p = 0.0002$ , d.f. = 7). It seems unlikely that this result is due to latitudinal effects. Although threatened species do have more southerly breeding ranges, on average, than do non-threatened species (mean latitudinal mid-point for threatened species =  $3^{\circ}$  S, for non-threatened species =  $1.5^{\circ}$  N; ANOVA,  $F_{1,3674} = 26.7$ ,  $p < 0.0001$ ), the difference is relatively small. Unfortunately, most latitudinal rows on the WORLDMAP grid do not include the mid-points of enough threatened migrant species to make statistical analysis by row meaningful.

Residents are more likely to be under threat in more than twice as many taxa than migrants (110 versus 48), although there are a further 67 taxa in which there is no relation between migration and threat. Thus, the hypothesis of a relation between migration and threat is not supported within taxa (two-tailed binomial  $p = 0.78$ ).

4. DISCUSSION

The geographic range sizes of New World birds are mainly small, giving the right-skewed frequency distribution of range sizes seen in most animal assemblages (Gaston 1994*a*). Logarithmic transformation, however, does not normalize this distribution; rather, on a logarithmic scale, range sizes are skewed away from the smallest sizes. Pagel *et al.* (1991) noted that the logarithmically transformed geographic range sizes for North American mammals appeared normally distributed, but truncated at larger sizes due to the limits imposed by the size of the area of study. The

Table 3. *The mean log<sub>10</sub> breeding range size of migrant (mean migrant) and resident (mean resident) New World birds in each row of the WORLDMAP grid*

(Latitude = latitudinal mid-point of the WORLDMAP grid row (All = all rows included in analysis). Note that because the grid is equal-area, but lines of longitude converge at the Poles, rows at high latitudes cover a wider latitudinal range than do rows at low latitudes; hence, latitudinal mid-points for rows are not equally spaced.  $F$  = F-ratio from ANOVA, d.f. = degrees of freedom. Analysis was restricted to latitudinally unrestricted (see Methods), endemic landbirds.)

latitude	mean migrant	mean resident	$F$	d.f.
all	0.94	0.58	138.30 <sup>c</sup>	1,3518
−55.36	1.12	1.11	0.03	1,54
−47.34	1.03	1.16	0.80	1,41
−40.44	1.08	0.93	3.74	1,94
−34.21	0.86	0.83	0.14	1,75
−28.41	0.63	0.56	0.28	1,62
−22.92	0.69	0.23	7.89 <sup>b</sup>	1,176
−17.64	0.96	−0.13	26.74 <sup>c</sup>	1,225
−12.52	0.67	0.002	4.71 <sup>a</sup>	1,241
−7.48	0.92	0.33	5.45 <sup>a</sup>	1,324
−2.49	1.39	0.74	17.26 <sup>c</sup>	1,393
2.49	1.21	0.90	1.30	1,330
7.48	1.30	0.87	3.16	1,567
12.52	1.03	0.72	3.01	1,299
17.64	0.71	0.66	0.10	1,198
22.92	0.78	0.63	2.57	1,211
28.41	0.74	0.60	2.67	1,131
34.21	0.53	0.38	1.26	1,44
40.44	0.39	0.19	1.85	1,13

<sup>a</sup>  $p < 0.05$ , <sup>b</sup>  $p < 0.01$ , <sup>c</sup>  $p < 0.0001$ .

pattern in the New World bird distribution cannot be due to truncation of this form. No bird species has a geographic range that covers the entire New World land area. The most widely distributed is *Falco sparverius* (L.), which is found in 84 % of grid squares, and breeds in 82 %.

Across all species, New World birds show a roughly triangular relation between range size and body mass, with small-bodied species displaying both small and large geographic range sizes, but large-bodied species tending to have only large ranges. The pattern is strengthened if species threatened with extinction are removed (figure 4). Thus, this assemblage supports previous suggestions that range size–body size relations will generally be positive when examined over areas encompassing the entire geographic ranges of most species in the analysis (Gaston & Blackburn 1996*a*), and that geographic range size–body size relations generally may be triangular in form (Brown & Maurer 1987, 1989).

A triangular relation between geographic range size and body size has been hypothesised to arise from constraints setting each of the three sides (e.g. Brown & Maurer 1987). At least four mechanisms could determine the position of the hypotenuse (Gaston & Blackburn 1996*b*). Currently the most favoured is that the minimum geographic range size at a given body size is fixed by the area needed to support the minimum viable global population of a species of that body size (Brown & Maurer 1987, 1989; Taylor & Gotelli 1994). It follows from this that species nearer to the hypotenuse should be closer to their minimum viable global population sizes, and that species below the hypotenuse may be below that minimum.

Our data show some support for this. Species considered to be under threat of extinction (Collar *et al.* 1994) show the same regression slope as unthreatened species for the range size–body mass relation, but with the slope elevation displaced towards the hypotenuse (see Results). Nevertheless, the high degree of significance for this result should be tempered by the obvious non-linearity of the relation between range size and body size in unthreatened species (figure 4*a*). The hypotenuse also appears to be more clearly defined when threatened species are excluded (compare figures 3 and 4), although this can only be a subjective statement in the absence of appropriate statistical techniques.

One of the other hypotheses proposed to explain the hypotenuse also receives some support from our analyses. This suggests that minimum range size may increase with body size because, on average, larger-bodied species disperse more rapidly and successfully (i.e. manage to establish) than small-bodied. Larger-bodied species may therefore occupy a greater proportion of their potential range sizes (the geographic range which could be occupied were all barriers to dispersal to be overcome; Gaston 1994*a*; Gaston & Blackburn 1996*b*). Evidence from New World birds indicates that birds that undergo migratory movements have larger breeding range sizes and body masses, on average, than do sedentary species. Although this hints at an effect of dispersal ability on the range size–body

size relation, it remains to be proven whether migratory species occupy a greater proportion of their potential range than do non-migrants.

The constraints determining the other two boundaries to the range size–body size relation have been less controversial, the vertical boundary apparently being set by the minimum body size possible for a taxon, and the horizontal boundary by the maximum land area available for colonization (Brown & Maurer 1987). These boundaries are well defined in New World birds, but both the frequency distributions of range size and the range size–body mass plots (figures 2–4) show that the upper horizontal boundary is not set by land area. This result is particularly intriguing because the upper boundary of the triangle is still approximately horizontal: what determines the maximum range size for a given body size seems to be constant across body sizes. At least two of the ‘species’ that have apparently escaped this boundary (*Vireo olivaceus* L., *Troglodytes aedon* Vieillot) may actually consist of more than one valid species (Ridgely & Tudor 1989; Sibley & Monroe 1990; Howell & Webb 1995).

If the amount of land area available does not generally determine maximum range size (land area must still set an absolute upper limit, but it is clear that ranges do not reach this limit), what does? Possible answers include the environmental tolerances of species (Root 1988*a, b*), biotic interactions (Repasky 1991), or the interaction of both (reviewed by Hoffmann & Blows 1994). Even very widely distributed species are not distributed through the very highest latitudes of North America (see e.g. del Hoyo *et al.* 1992; 1994). Perhaps the degree of specialization required to be able to breed at the continental extreme prevents occupation of these latitudes by species of more generalist nature; in other words, no species is generalist enough to occupy all habitats, and so must be limited to some degree by the distribution of habitats that are suitable. Whether this would produce a body size invariant range size limit is debatable, and distinguishing between the mechanisms that may limit species distributions is difficult (Repasky 1991; Hoffmann & Blows 1994). Whatever the mechanism, though, it does not produce consistent range size–body size relations within taxa. This perhaps suggests that it is more eclectic than ‘simple’ environmental constraints.

Species of different migratory status are not distributed at random with respect to the distributions of range size and body size, nor with respect to latitude. Migrant species tend to have larger geographic ranges than resident species, and to be larger-bodied, with some suggestion that the former does not simply result from the latter and the overall range size–body size relation. The fact that migrant species have larger geographic range sizes is unsurprising, although at least when study areas do not embrace species’ entire geographic ranges, this need not be so (O’Connor 1981; Cotgreave 1994). Their larger geographic ranges are not simply the result of their more northerly breeding distributions, because they tend to have larger range sizes than residents at any given latitude (table 3).

It has been postulated that migrant species tend to

be habitat generalists, in order to exploit the different geographic areas in which they breed and winter (Rappole *et al.* 1994 and references therein). This concurs with a more general argument that widespread species are more generalist than are restricted species (Brown 1984), although evidence for this position remains equivocal and poorly distinguished from the evidence that widespread species simply exploit more widespread resources (Gaston 1994a). If in addition to having larger geographic ranges, migrant species are indeed more generalist, it remains to ascertain whether their generalism enabled them to become migrants or whether the selection pressures associated with their migratory behaviour resulted in them becoming generalist.

The patterns of geographic range size observed across latitudes are intriguing. They are similar when analysed using four different methods, although the details observed vary and we needed to manipulate the data to allow patterns to be observed within taxa. Surprisingly, all methods indicate that minimum range size is not attained by species with their latitudinal mid-points at the equator, but rather at about 17° N, around the latitudes of southern Mexico and northern Central America (figure 5a, 6a, 7a). This is close to the latitude at which the continental New World is at its smallest longitudinal extent. However, the pattern is not a simple consequence of land area. Species with latitudinal mid-points in Central America are not inherently restricted to this small isthmus. Rather, a species with its mid-point at 17° N can potentially have a geographic range spanning about 120° of latitude and covering most of the land area of the New World. Indeed, many of the species distributed through Central America have very large geographic ranges, although rather few of them have their range mid-points there. Thus, species with latitudinal range mid-points either side of 17° N tend to utilize much more of the entire land mass available to them than do species at this latitude (figure 5b, 6b, 7b; species at all latitudes can potentially attain a value of 1 on the ordinate in these plots).

At present, this is the only plot of geographic range size against latitude that crosses a wide enough range of latitudes to demonstrate such a relation, at least for terrestrial taxa. Studies on marine teleosts (Rohde *et al.* 1993; Macpherson & Duarte 1994) and elasmobranchs (Macpherson & Duarte 1994) have encompassed a similar range of latitudes, but show no consistent relation between range size and latitude. Thus, the generality of our result is uncertain. Nevertheless, in this context, it is interesting that both Pagel *et al.* (1991) and Letcher & Harvey (1994) detected sigmoidal latitudinal patterns in geographic range size, in Nearctic and Palearctic mammals respectively: that is, range size did not reach a minimum at the lowest latitudes (see also figure 1 in Stevens (1989) for freshwater fish in North America). The former study encompassed latitudes south to about 10° N, the latter to about 20° N. Pagel *et al.* (1991) attributed this pattern to continental shape, whereas Letcher & Harvey (1994) suggested that it might be an artefact of the method of analysis used (the same as 'Stevens'

method' here). In view of the patterns we observe, a possible reinterpretation could be that mammals also attain minimum range sizes north of the equator. We would also note that latitudinal patterns are most strongly expressed using Stevens' method, because of autocorrelation. Given that 17° N is close to the southern limit of the area in the two mammal studies, this may be why it is only this method that detects the up-turn in range sizes in these studies. Finally, the pattern observed in plots of latitude against geographic range size will depend on the range of latitudes across which a study is performed. Positive, negative or no relation between these two variables could be extracted from figure 5 by analysis of only part of the latitudinal range.

The pattern we demonstrate across all latitudes for New World birds, both across species and within taxa, has important consequences for hypotheses attempting to explain Rapoport's rule. The most frequently cited mechanism is the climatic variability hypothesis (see Stevens 1989, 1992a, b; France 1992; Letcher & Harvey 1994; Smith *et al.* 1994). It argues that species living further from the equator will generally experience a much wider range of climatic conditions than will equatorial species. Therefore, they will be selected to be generalist to cope with this wider range of conditions. Because generalists are not restricted to certain habitat types, these species will have larger geographic ranges than equatorial species, and hence a relation arises between latitude and geographic range size (Stevens 1989). From this, it follows that measures of climatic variability and range size should be correlated, and hence, from our data, that climatic variability should be lowest between 10° and 20° N.

Data on latitudinal variation in climatic variability presented by Stevens (1989) do not support this assertion. However, these data were not compiled specifically for the New World. The issue is also complicated by altitudinal range. Stevens (1992b) has demonstrated that a Rapoport effect exists for altitude, as well as latitude, with species occurring at higher altitudes also residing over a greater altitudinal range. Patterns of geographic range size in the New World may be confounded by the wide range of altitudes in equatorial regions generated by the Andean mountain range. Nevertheless, the patterns we demonstrate will have to be adequately accounted for by any hypothesis that purports to explain Rapoport's rule. We are not convinced that any single current hypothesis is sufficient.

We suggest that the distinct latitudinal pattern in geographic range sizes of New World birds is not due to climatic variation, but rather is the consequence of the biogeography of the New World. Central America marks a zone of floristic change. The humid, lowland rainforest typifying much of equatorial South America reaches its northern limit around southern Mexico (e.g. southern Veracruz and northern Oaxaca, Yucatan peninsula; Leith & Werger 1989; Groombridge 1992). Likewise, northern forests reach their southern range limit around this point (e.g. conifers extend no further south than Honduras and western Nicaragua). It would be expected from this

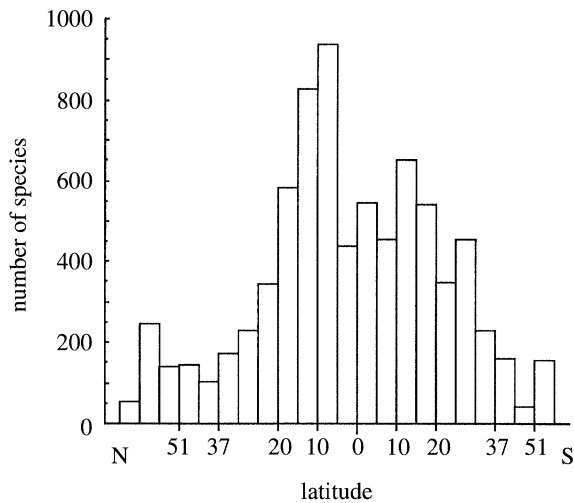


Figure 8. The frequency distribution of latitudinal range limits across rows of the WORLDMAP grid. The grid includes 22 latitudinal rows. The histogram shows the number of species that have either their northerly or southerly range limit in each row. Latitude is to the nearest degree. Note that because the grid is equal-area, but lines of longitude converge at the Poles, rows (and hence histogram bars) at high latitudes cover a wider latitudinal range than do rows at low latitudes.

that many bird species show similar range limits. This indeed seems to be the case. The main tract of tropical rain forest in northern Central America (the Olancho forest) extends through central Honduras to its caribbean north coast. Howell & Webb (1995) exclude from their guide to the birds of Mexico and northern Central America 50 species which have their northern range limit in the Olancho. They also note that most temperate zone species reach their southern range limits in the north of the highlands of Honduras and western Nicaragua. It seems reasonable to conclude that there is a general turnover in the avifauna around southern Mexico and northern Central America, at about latitude 17° N. Some evidence for this hypothesis is given in figure 8, which shows that large numbers of bird species do indeed have either their northerly or southerly range limits at about this latitude (although this is not the only latitude with a high density of range limits). In addition, Gauld & Gaston (1995) show that this is also a region of faunal turnover for Hymenoptera.

The consequences of this faunal turnover for the geographic range sizes of birds in this region are obvious. Many species from the southern rainforests have their northern range limits at about this latitude (and vice versa for northern forest species). These species will only have their latitudinal mid-points in this region if they also have very small geographic ranges. Conversely, if these species have large geographic ranges, their latitudinal mid-points will be south (or north) of this region. Therefore, species which do have their mid-points around 17° N will tend to have very small ranges only, whereas species with larger ranges will not have their mid-points there. The tendency for Central American forest species to have

small geographic ranges will be further exacerbated by the well-known biogeographic disjunction signalled by the high number of avian taxa that are endemic to the region defined by southern Central America and the Chocó region of northwestern South America (Haffer 1967; Cracraft & Prum 1988). Some species do have their latitudinal mid-points here and large geographic ranges (figure 5). There are many widely distributed species that are not restricted to certain biogeographic regions (e.g. habitat generalists, human commensals, coastal species), and it is expected by chance that some of these should have their latitudinal mid-points around 17° N.

The potential importance of biogeographic structure in determining patterns in range size has been suggested by Roy *et al.* (1994). They found no relation between latitudinal range size and latitude in Eastern Pacific molluscs, but rather that the former seemed to be set by the influence of major oceanographic barriers. Whether climatic variation interacts with range size within biogeographic regions, either in molluscs or in New World birds, remains unresolved. Such an interaction will be difficult to demonstrate, because biogeographic regions show less climatic variation, and can apparently exert influences similar to those exerted by edges to land masses. Thus, it will be difficult to determine whether range limits are set by climate or by biogeography, and these will anyway often be inter-related.

How reliable are the patterns revealed by these data? The data will surely contain sources of error, and range sizes will generally be overestimated. One possible systematic bias would be if the apparent geographic ranges of equatorial species were inflated by the extreme linearity of the ranges of many Andean birds (Graves 1985, 1988). These ranges may actually be rather small but, because of their sinuous form, fall in a large number of grid squares. However, it is extremely unlikely that this effect alone produces the large mean range size observed for equatorial New World birds. Many lowland equatorial species are widely distributed through Amazonia. For mean range size to decrease from 17° N to the equator would require the lowest latitudes to be stocked predominantly with narrow-range endemics. Although Amazonia does include a number of areas of endemism (Cracraft & Prum 1988; Haffer 1988), this is clearly not the case (see e.g. Ridgely & Tudor 1989, 1994). Further, analysing distributional ranges using latitudinal extents, as does Stevens (1989), would probably result in even larger apparent ranges for Andean birds. In sum, we do not think our failure to detect Rapoport's rule in New World birds is the result of biases in the data.

Although we think that there are no systematic biases that alone are likely to cause the patterns we observe, certain features of the data, and the way in which they have been analysed, may heighten the underlying patterns. First, the latitudinal mid-points of species with ranges in one hemisphere are shifted towards the Pole of the hemisphere in which they occur (see Methods). Because this effect is likely to be greater for species with larger ranges, it too could exaggerate a



Rapoport effect. However, the effect is small for species with latitudinal mid-points at low latitudes, and in particular could not bias mid-point positions enough to produce the observed tendency for range size to be smallest at around 17° N.

Second, the range sizes we use are scaled by the amount of land area in each grid square in which a species' range falls. Hence, a species which occupies a single square will have a range size of one if the square is entirely covered by land, but only 0.5 if land covers only half of the square. Species with ranges restricted to one square in Central America, for example, will therefore appear to have smaller geographic range sizes than species with ranges restricted to one square in Amazonia, because squares in Central America contain less land area. This may contribute to the pattern in figure 5a by setting a lower minimum range size between 10 and 20° N. However, the relation in figure 5a remains if range sizes are not scaled by the amount of land area in a square, albeit it is less clearly defined.

A similar problem also affects the proportion of the total land area available to a species with a given latitudinal mid-point that the species actually uses. Although the maximum is always unity, when a species uses all the area available, the minimum value depends partly on how many squares are actually available, and hence on latitude. Thus, if species at all latitudes used the same land area, those with latitudinal mid-points in the tropics would be seen to use a lower proportion of the area available. However, the importance of this point is reduced by the coincidence of the smallest range sizes and the smallest proportions of available area used at the same latitudes. The pattern in figure 5b is not an artefact of a constant minimum range size. Moreover, such an artefact cannot explain why so many species with mid-points around 17° N use such a small proportion of the land area available to them, relative to latitudes both to the north and south.

Finally, a spurious Rapoport effect may arise as a consequence of higher species diversity in tropical regions (Colwell & Hurtt 1994). This is a general possibility in latitudinal analyses of geographic range size patterns, and not a specific consequence of our methods. It arises because high tropical diversity means that much higher levels of sampling are required in tropical regions to detect all the species present in a given area, whereas the faunas of these areas are actually much less well known than those of temperate regions. Range sizes of tropical species hence may be consistently underestimated (see also Gaston *et al.* 1996). This is an interesting possibility, especially given that it has previously been suggested that species richness gradients and Rapoport's rule share a common biological cause in the climatic variability hypothesis (Stevens 1989). Both the artefactual and biological hypotheses imply coincidence of gradients in range size and species richness. However, such an artefact is unlikely to contribute strongly to the patterns of geographic range size observed for New World birds, given the low resolution of the mapping employed. An analysis of species richness patterns in New World birds is beyond the scope of this work, but is addressed in a subsequent paper (Blackburn & Gaston 1996a).

We thank Ros Jones for collating data on endemism in New World birds, Linda Birch, John Lawton, Natasha Loder and Effie Warr for assistance with data sources, Mark Pagel for the evolutionary covariance method program, Paul Williams for help with the WORLDMAP program, Dieter Ebert and Christophe Thebaud for helpful discussions on methodology, and Richard Gregory, John Lawton, Adrian Long, Paul Williams, Mark Williamson and an anonymous referee for comments that materially improved this work. T.M.B. was supported by NERC grants GR3/8029 and GST/03/1211. K.J.G. is a Royal Society University Research Fellow.

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Received 27 November 1995; accepted 10 January 1996