Scaling in the growth of geographically subdivided populations: invariant patterns from a continent-wide biological survey

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We consider statistical patterns of variation in growth rates for over 400 species of breeding birds across North America surveyed from 1966 to 1998. We report two results. First, the standard deviation of population growth rates decays as a power-law function of total population size with an exponent $\beta = 0.36 \pm 0.02$. Second, the number of subpopulations, measured as the number of survey locations with non-zero counts, scales to the 3/4 power of total number of birds counted in a given species. We show how these patterns may be related, and discuss a simple stochastic growth model for a geographically subdivided population that formalizes the relationship. We also examine reasons that may explain why some species deviate from these scaling laws.

Keywords: invariant scaling; population variability; Taylor's power law; population ecology; North American breeding bird survey

1. INTRODUCTION

Perhaps one of the most intriguing patterns in ecology is Taylor's law (Anderson *et al.* 1982; Soberón & Loevinsohn 1987; Routledge & Swartz 1991; Leps 1993; Curnutt *et al.* 1996; Maurer 1999). Taylor (1961) was the first to notice that when the mean $<S>$ of a population survey is plotted versus its variance $\sigma^2(S)$, either in space or time, the relationship is typically a power law with a fractional exponent

$$\sigma^2(S) \propto <S>^\gamma. \tag{1.1}$$

Taylor was originally interested in the slope of the power-law relationship as a scale-free measure of spatial contagion or dispersion—values greater (less) than one indicate spatial clustering (over-dispersion). Later, Taylor used both spatial and temporal scaling as a basis for comparative studies of, in his words, 'synoptic population dynamics' across taxonomic groups (Taylor & Woiwod 1982; Taylor 1984).

Taylor's synoptic approach is, in many respects, a precursor to the recent development of 'macroecology' (Brown 1995), a sub-discipline of ecology and biogeography (MacArthur & Wilson 1967) that seeks to identify broad patterns in species' abundance and distribution. Macroecology has largely focused on static patterns, such as spatial relationships between abundance and environmental factors (Brown *et al.* 1995)

and relationships between metabolic energy use and geographical distribution (Brown & Maurer 1987). Thus, relatively few continental-scale macroecological studies (Maurer 1994, 1999) have explored interactions between spatial distribution and population variability through time.

In this paper, we adopt Taylor's synoptic approach and analyse one of the most comprehensive macroecological datasets available, the North American breeding bird survey (Peterjohn 1994). The data are estimates of local abundance (counts) for over 600 bird species recorded at 2000–3000 sites (routes) across North America for the years 1966 to 1998. Unlike many previous macroecological studies, our focus is on linking geographical distribution to population dynamics. We report two new scaling laws, closely related to Taylor's power law, for these data: one relating variability of population time-series to their mean, and another relating number of sites occupied to total population size. In addition, we show how these patterns may be related, and discuss a simple stochastic growth model for a geographically subdivided population that formalizes the relationship.

2. SCALING OF SPECIES GROWTH RATES

Our goal is to understand temporal variation in abundance at the entire population level. We therefore compute time-series of total counts for each species by summing over all routes surveyed in a given year (figure 1a). (We have previously analysed these data at the individual route level; see Keitt & Stanley 1998.) The aggregated time-series should be relatively robust to observer errors inherent in the route-level data (Kendall *et al.*

Phil. Trans. R. Soc. Lond. B (2002) **357**, 627–633
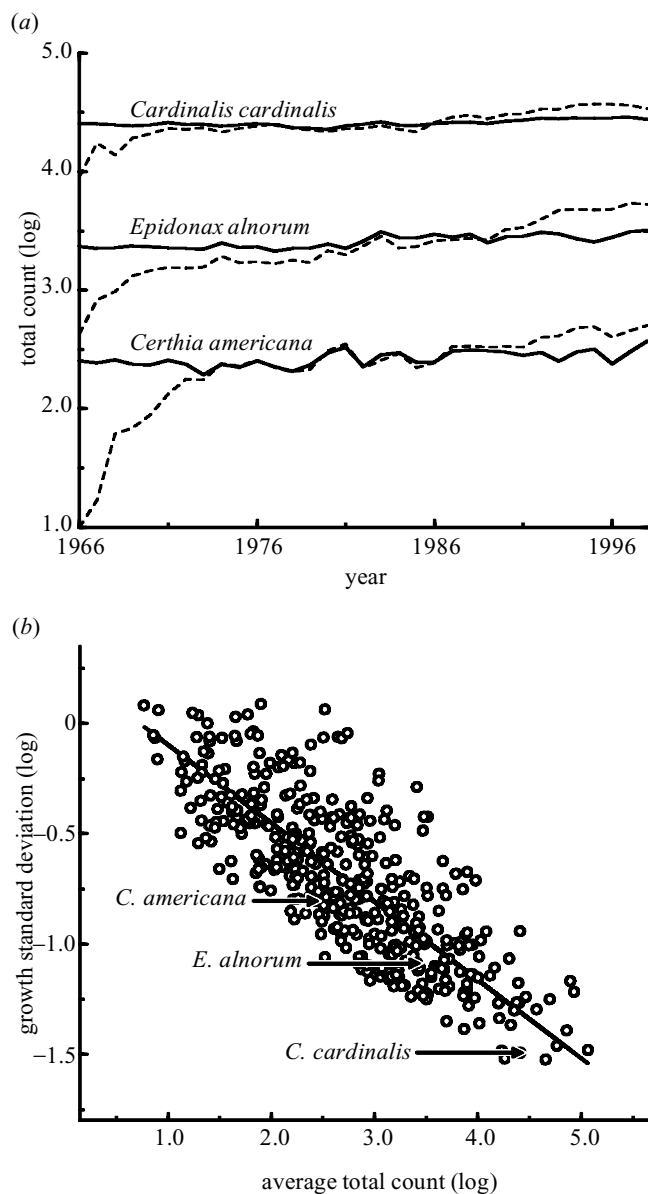DOI 10.1098/rstb.2001.1013

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(a)

(b)

Figure 1. Scaling of ecological time-series. (a) Time-series of total counts for three species of birds (northern cardinal (*Cardinalis cardinalis*), alder flycatcher (*Epidonax alnorum*) and brown creeper (*Certhia americana*)). Dashed lines show the uncorrected total number of birds counted in a given year. Solid lines are bias-corrected totals (see text for explanation). (b) Standard deviations of empirically observed population growth rates plotted against average annual total counts for 428 species of North American breeding birds. Results for the time-series plotted in (a) are highlighted. Notice that the highlighted time-series are less variable than other species in the dataset with similar total population size.

1996), as random undercounts and overcounts will cancel in the summation. After performing a bias correction (see Appendix A for details), the resulting time-series are relatively free of systematic trends, particularly in the early years of the survey when the number of routes was increasing rapidly (compare dashed with solid lines in figure 1a).

We choose as our measure of the magnitude of time-series fluctuations the logarithm of the ratio of successive counts,

$$g(t) \equiv \log\left(\frac{S(t+1)}{S(t)}\right),\tag{2.1}$$

where $S(t)$ and $S(t+1)$ are the total numbers of birds of a given species counted in years t and $t+1$, respectively. This measure has several good properties. First, any multiplicative, time-independent sample bias cancels in the ratio. Second, the measure has a natural interpretation in terms of population demography as, in a closed population, $\exp[g(t)] \approx 1 +$ (per capita birth rate − per capita death rate).

As shown in figure 1b, the standard deviation $\sigma(g)$ of population growth rates is strongly related to the average total population size. The relationship follows a power law

$$\sigma(g) \propto <S>^{-\beta},\tag{2.2}$$

for over four orders of magnitude in $<S>$, the total count averaged across years. For these analyses, we are not interested in predicting a 'dependent' variable from an 'independent' variable. Rather, we are interested in modelling the functional form of the interdependence among variables. We therefore use major-axis regression (Sokal & Rohlf 1995) to estimate model parameters. Major-axis regression is based on computing the leading eigenvector of the covariance matrix, and minimizes squared errors measured perpendicular to the trend line. We also restrict our analysis to non-zero time-series of at least 25 years in length and with a minimum average total count of no fewer than five birds per year. Using major-axis regression with bootstrap precision estimates, we find $\beta = 0.36 \pm 0.02$. Taylor's exponent (here replicated across species) is then simply $\gamma = 2(1 - \beta) = 1.28 \pm 0.04$.

We also study the scaling properties of population growth rates by examining changes in the distribution of growth rates with increasing population size, a technique familiar to statistical physicists. First, we separate the observed growth rates into three bins according to the total count $S(t)$ and then construct a histogram to estimate the conditional probabilities $p(g|S)$. The resulting distributions are roughly triangular in shape with the width depending on S (figure 1a). (The triangular shape may result from summing over a large number of time-series with different local variances; see Amaral *et al.* (1998).) If the distributions are 'self-similar' (i.e. exhibit scaling), then we should be able to identify a function f that rescales the distributions so that they 'collapse' onto each other. We plot the scaled quantities

$$\sigma(S)p\left(\frac{g}{\sigma(S)}\Big|S\right) \text{ against } \frac{g}{\sigma(S)}\tag{2.3}$$

(figure 2a) and find that the three curves do indeed collapse onto each other (figure 2b), suggesting that $p(g|S)$ follows a universal scaling form

$$p(g|S) \propto \frac{1}{\sigma(S)}f\left(\frac{g}{\sigma(S)}\right).\tag{2.4}$$

These results are interesting for a number of reasons. In statistical physics, the presence of non-trivial scaling is usually taken to mean that the dynamics is largely gov-
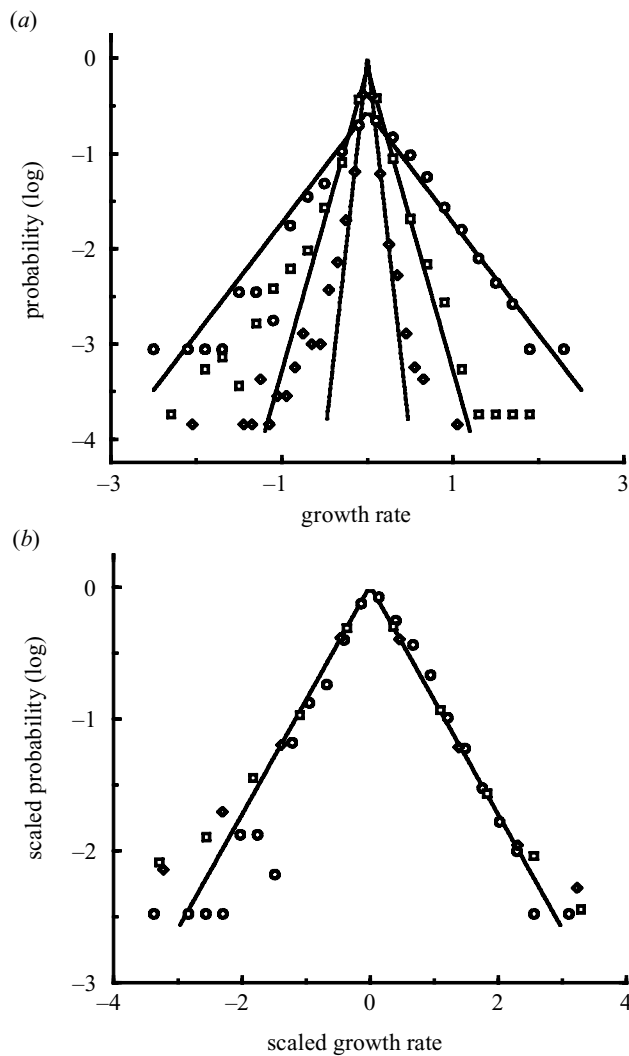
Figure 2. Distribution of growth rates for different population size classes. (*a*) Probability density $p(g|S)$ of the growth rate g for all bird species in the North American breeding bird survey database. The distribution represents all annual growth rates observed in the 31 year period 1966–1996. We show the data for three different bins of initial sizes (circles, $10^0 < S(t) < 10^1$; squares, $10^1 < S(t) < 10^{2.4}$; diamonds, $10^{2.4} < S(t) < 10^{3.8}$). The solid lines are exponential fits to the empirical data close to the peak. The approximately triangular shape of the distribution may be the result of mixing Gaussians of different widths (Amaral *et al.* 1998). (*b*) Scaled probability density $p_{scal} \equiv \sigma p(g|S)$ as a function of the scaled growth rate $g_{scal} \equiv [g - \bar{g}]/\sigma$ for all species and years in the survey. The values were re-scaled using the measured values of $\bar{g}$ and σ. All the data collapse upon the universal curve $p_{scal} = f(-|g_{scal}|)$.

erned by simple geometric properties of the system and does not depend strongly on detailed properties of the system subcomponents (Wilson 1983). Thus, it is remarkable that we should find strong evidence for scaling across such a taxonomically and ecologically diverse set of species as found in the North American breeding bird survey. These results suggest that the dynamics of North American breeding birds is unexpectedly 'simple' and depends primarily on common patterns of internal population structure across species ranges, rather than details of individual species' life histories.

3. SPATIAL STRUCTURE OF SUBPOPULATIONS

Another reason that the growth-scaling results are interesting is the large variability of highly abundant species. Imagine the null model that each population is subdivided into n equally sized, independent subpopulations, and that the number of these subpopulations depends linearly on S. The expectation, according to the central limit theorem, is that the standard deviation in growth rates should decay as the $-1/2$ power of S. The observed decrease in fluctuations is considerably slower (i.e. $\beta < 1/2$), such that highly abundant species are considerably more variable than expected under the null model.

To account for the increased variability for highly abundant species, we require that the number of subpopulations does not scale in a simple, linear fashion with increasing S, but instead takes the form

$$n \propto S^{1-\alpha}, \tag{3.1}$$

with $\alpha \neq 0$. Values of $\alpha > 0$ will be found, for example, when the 'typical' size of the subpopulations also scales with total abundance, i.e. there is a positive relationship between regional and local abundance, a well-documented pattern in macroecology (Gaston & Lawton 1988; Gaston 1996). The positive correlation between local and regional abundance results in fewer subpopulations for a given total population size as each subpopulation accounts for more individuals. Again appealing to our observation that, under the central limit theorem, $\sigma(g) \propto n^{-1/2}$, and in combination with equations (2.2) and (3.1), it is straightforward to show that for roughly equal-sized subpopulations, the estimated exponents must obey

$$\beta = \frac{1-\alpha}{2}. \tag{3.2}$$

We do not have access to a precise estimate of the number of subpopulations for each species in the survey. However, we can use as a proxy the number of survey routes where a species had a non-zero count in a given year. To test the assertion in equation (3.2), we plot the number of survey routes with non-zero counts $\tilde{n}(t)$ versus the (uncorrected) total count $S(t)$ for all bird species recorded in the survey in 1997, excluding species seen at fewer than five routes or with fewer than five total individuals counted. The data follow closely the power-law dependence predicted by equation (3.1) with an exponent $\alpha = 0.25 \pm 0.03$, again using major-axis regression with bootstrap precision estimates (figure 3*a*). Remarkably, the estimate of α predicts a value of $\beta = 0.38 \pm 0.02$, very close to the estimate ($\beta = 0.36 \pm 0.02$) obtained by measuring the standard deviation in growth rates directly (figure 1*b*). Even more striking is the consistency of our estimate of α across the years, despite large changes in the number and spatial distribution of sampling locations through time (figure 3*b*). These results directly imply that average local abundance $<S> = S(t)/\tilde{n}(t)$, scales with total (regional) abundance according to $<S> \propto S(t)^\alpha$.

We can gain further insight into the organization of a species population in different routes by considering how the distribution of number of routes with non-zero counts depends on total counts. That is, we may quantify the organization of the subpopulations through the conditional probability density $\rho(\tilde{n}|S)$, which measures the
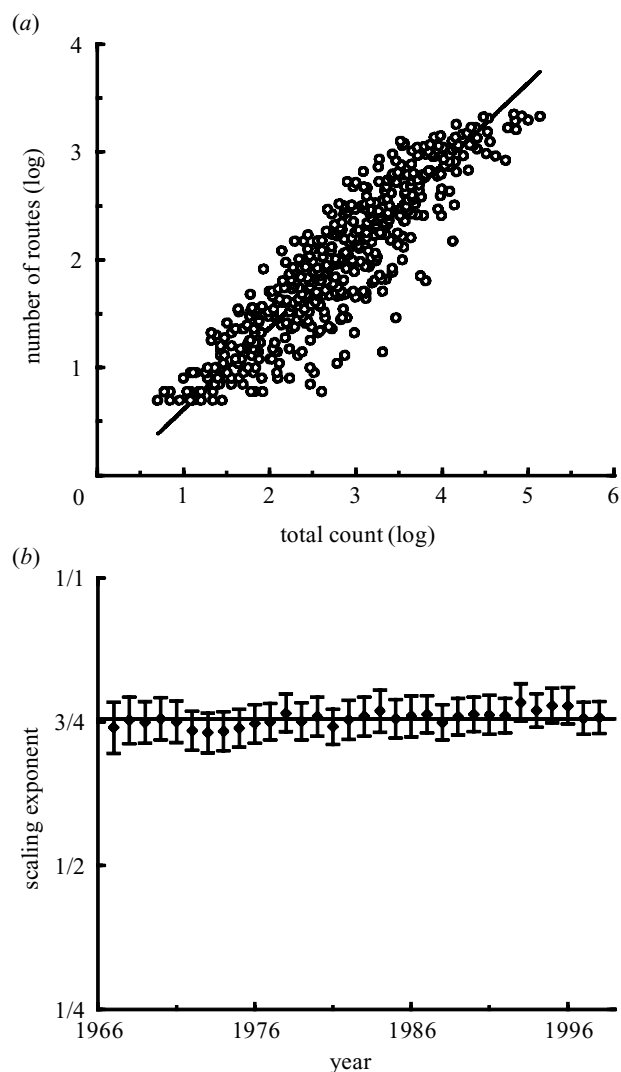
(a)

(b)

Figure 3. Statistical analysis of the number of routes populated by a given bird species. (a) Double logarithmic plot of the number of routes with non-zero counts $\tilde{n}(t)$ versus total number of birds counted $S(t)$ for each species observed in 1997. The bias correction applied to the time-series in figure 1 is unnecessary in this case as all data come from a single year. The data for all species closely follow a straight line, the log–log plot suggesting a power-law dependence. From the slope of the line, we estimate $1 - \alpha = 0.75 \pm 0.03$. (b) We performed a similar analysis for all 31 years in the database and plotted the exponent estimates for each of the years. Our results show that the power-law dependence remains remarkably stable during the 31 survey years, clustering around $\alpha = 0.25$. Error bars are bootstrap 95% confidence intervals.

probability of finding a bird species with S total counts having non-zero counts in $\tilde{n}$ distinct routes. Figure 3 suggests that $\rho(\tilde{n}|S)$ will have a peak that increases as a power law with S. As shown in figure 4a this is indeed the case. If the data exhibit scaling, we should be able to identify a universal scaling function h such that

$$\rho(\tilde{n}|S) \propto \frac{1}{S^{\alpha}} h\left(\frac{\tilde{n}}{S^{\alpha}}\right).$$

(3.3)

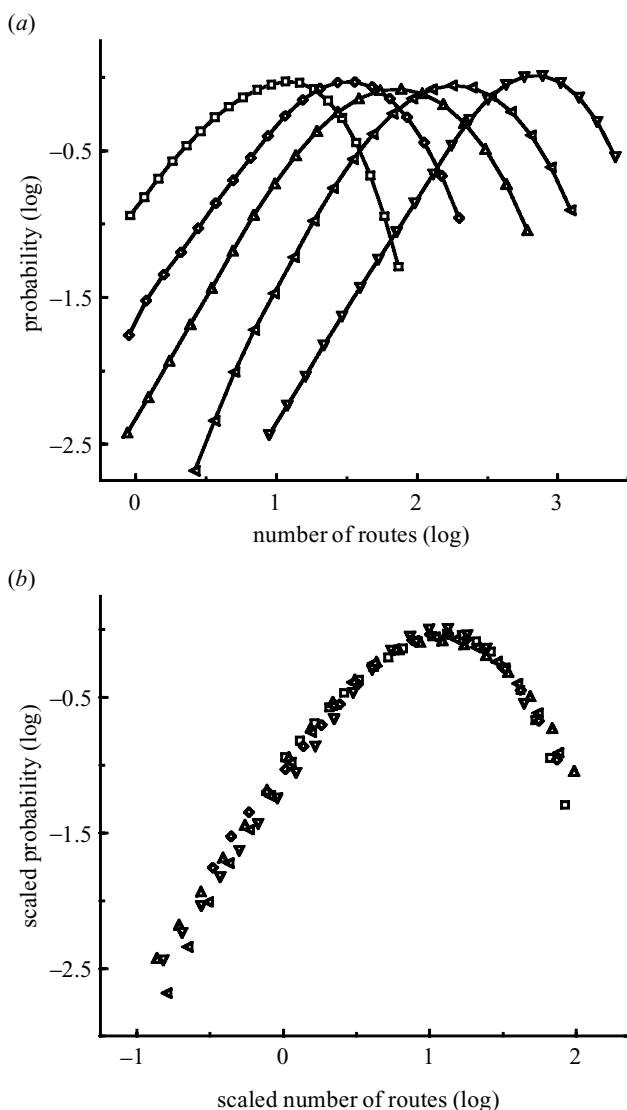We test the scaling hypothesis in equation (3.3) by plotting the scaled variables

(a)

(b)

Figure 4. Statistical analysis of the number of routes populated by a given bird species. (a) Conditional probability density function $\rho(\tilde{n}|S)$ of finding $\tilde{n}$ non-zero count routes for a bird species with S total counts. To improve the statistics, we partitioned the bird species into five groups according to size (squares, $10^{1.2} < S < 10^{1.9}$; diamonds, $10^{1.9} < S < 10^{2.4}$; upright triangles, $10^{2.4} < S < 10^{2.9}$; left pointing triangles, $10^{2.9} < S < 10^{3.5}$; down pointing triangles, $10^{3.5} < S < 10^{5.2}$). (b) To illustrate the scaling relation (equation (3.3)), we plot the scaled probability density $S^{1-\alpha} \rho(\tilde{n}/S^{1-\alpha}|S)$ versus the scaled number of non-zero routes $\tilde{n}/S^{1-\alpha}$, combining data from all years. In agreement with equation (3.3), we find that the scaled data fall onto a single curve.

$$S^{\alpha} \rho\left(\frac{\tilde{n}}{S^{\alpha}} \Big| S\right) \text{ against } \frac{\tilde{n}}{S^{\alpha}}.$$

(3.4)

Figure 4b shows that all curves collapse onto a single curve, which yields the scaling function $h(u)$.

4. DISCUSSION

Our analysis differs from Taylor's original studies (Taylor 1961, 1984; Taylor & Woiwod 1982) in an important way. Taylor was interested in comparative analysis and so calculated a separate exponent for each

species. He did this by analysing multiple samples, replicated across time or space, for each species. Here, we calculate exponents replicating *across* species. One advantage of this approach is that we analyse the time-series of total counts, summed over the entire survey. These total counts are considerably more robust estimates of abundance than local counts taken at individual routes.

Another advantage of analysing scaling across species is that it allows us to separate general patterns or 'laws' that are invariant across taxonomic groups from general rules that may explain *deviations* from these laws. Our reasoning is that when the physical dimensions of a problem, such as energy or material flows, or spatial population structure, predominate, we should observe scaling laws that do not depend strongly on the biological differences among species, but that species-specific differences should appear as a residual variation after the common scaling laws are factored out. That so many species fall along a single scaling relationship describing variability as a function of population size (figures 1 and 2) suggests that there may be universal features to the way in which North American breeding bird populations are subdivided spatially. We find exactly these features in the invariant, 3/4-power scaling of number of occupied survey routes versus total population size (figures 3 and 4).

However, not all of the variability in the data is accounted for by these scaling laws. For example, species with average total counts of approximately 250 individuals exhibit more than two orders of magnitude range in growth-rate standard deviation (figure 1*b*). We believe that this residual variation does reflect important aspects of the ecology of individual species (see also Kolasa *et al.* 1996). There is a strong correlation between the residuals in figure 1*b* and the area of the corresponding species ranges, measured in terms of the average number of non-zero routes (T. Keitt, unpublished results). A probable explanation for this pattern is that fluctuations in the abundances of broadly distributed species will tend to average out spatially because different regions are influenced by geographically distinct climate regimes. Thus, it appears that species whose life histories tend to produce strongly aggregated distributions (i.e. species that are locally common but regionally rare) are the ones that fluctuate the most relative to their total abundance. Species that have broad spatial distributions (i.e. locally rare but regionally common) are therefore expected to fluctuate less than similar species with more restricted geographical ranges.

Ranking species in terms of their residual deviation from the growth-scale law (figure 1*b*) supports our hypothesis that locally common but regionally rare species fluctuate more than expected, and vice versa. Large positive residuals correspond to species with restricted geographical ranges, such as the golden-cheeked warbler (*Dendroica chrysoparia*; 2.5 times more variable), species that are habitat specialists and nest in large colonies, such as the tricoloured blackbird (*Agelaius tricolor*; 13.7 times more variable), species that breed in large groups called 'leks', such as the greater prairie chicken (*Tympanuchus cupido*; 3 times more variable), and species that show strong local migration patterns in response to changes in resource availability, such as the white-winged crossbill (*Loxia leucoptera*, 3.5 times more variable) and red crossbill (*Loxia pytyopsittacus*, 3.7 times more variable). Species that show

low variability in relation to the scaling law are typically solitary, territorial breeders such as the yellow-throated warbler (*Dendroica dominica*; 2.8 times less variable), prairie falcon (*Falco mexicanus*; 2.6 times less variable), swamp sparrow (*Melospiza georgiana*; 2.5 times less variable), Kentucky warbler (*Oporornis formosus*; 2.4 times less variable) and Chuck-will's-widow (*Caprimulgus carolinensis*; 2.3 times less variable). The important point is that had we started from a purely autecological standpoint and ignored the important physical dimensions of the problem (e.g. structure of geographical ranges), we could easily have missed key patterns in terms of deviations from general scaling laws.

We should, however, mention several caveats. We do not as yet know whether our results can be generalized to include other, non-avian taxonomic groups, or to other continents and climate regimes. Also, despite our use of highly aggregated, and therefore more robust, time-series, we suspect that there remain sources of variation in our analysis unrelated to actual population fluctuations. One vexing problem is repeated local migration between sampled and unsampled locations (we call this 'sloshing'). Even if there is no variation in the true abundance across years, sloshing will lead to a given individual being counted in some years and not others, leading to measurement errors in the time-series. We suspect this effect is not a significant component of variation in most of our time-series, but may be substantial in a few cases. (Sloshing may contribute to the extreme variability of the tricoloured blackbird, for example.) Additional data, such as mark–recapture, may be needed to resolve this issue.

There are two additional mechanisms related to our model for geographically subdivided populations that we have not discussed. We have shown how a nonlinear dependency of the number of subpopulations versus total population size may explain the observed deviation from 1/2-power scaling of population fluctuations. Our basic hypothesis depends on the average local abundance scaling with total abundance in independently fluctuating subpopulations of roughly equal size. However, there are other patterns that may influence the 'effective' number of independently fluctuating subpopulations, and thus partially amount for the observed exponent in the growth-scaling law. First, large spatial variation in local abundance (Brown *et al.* 1995) could cause widespread species to fluctuate with greater magnitude than if all subpopulations have the same local abundance, as most of the variation would be driven by a few, high-abundance sites. Second, strong spatial autocorrelation in population growth increments or 'spatial synchrony' among fluctuating subpopulations (Grenfell *et al.* 1998; Bjørnstad *et al.* 1999; Kendall *et al.* 2000; Lundberg *et al.* 2000) may also cause a reduction in the effective number of independent subpopulations, and thus account for the increased magnitude of fluctuation in broadly distributed species. Temporal autocorrelation may act similarly to increase or decrease variability relative to our model. The consequences of these mechanisms need further exploration.

A surprising result of our analysis is the, to our knowledge, previously unreported 3/4-power scaling of spatial distribution as a function of total population size (figure 3). This result is closely related to, but not the same as,

the 'distribution–abundance' curve of Hanski & Gyllenberg (1997) that describes the fraction of regional habitats occupied as a function of average local abundance. We do not as yet have an explanation for why the exponent should take this particular value, nor why it is so consistent through years. Recently, there has been considerable interest in explanations for the apparent 3/4-power scaling law relating body mass to metabolic output (Enquist *et al.* 1998; West *et al.* 1999; Dodds *et al.* 2001; Niklas & Enquist 2001). One explanation posited to explain 3/4-power scaling is optimal structuring of a fractal transport network, such as the vascular system of plants and animals (West *et al.* 1999). This suggests an interesting hypothesis to explain 3/4-power scaling in our analysis: if the geographical ranges of species are subdivided according to a particular fractal pattern, perhaps because of the fractal nature of the physical environment (e.g. Rinaldo *et al.* 1995), then it might lead to our observed scaling laws. Testing this hypothesis will require additional study.

It is interesting to note that our results are in striking qualitative agreement with similar studies from a broad range of social systems, ranging from growth of companies in the US economy to the GDP of countries (Stanley *et al.* 1996; Lee *et al.* 1998; Plerou *et al.* 1999), suggesting that our simple model of growth may apply quite broadly (Amaral *et al.* 1998). Our observation that more 'specialized' bird species (in terms of smaller number of subpopulations) fluctuate more than broadly distributed species may have an interesting parallel in social organizations: those that specialize in a few economic activities, e.g. countries with a single export product, may fluctuate considerably more than a similarly sized organization with diverse economic activities, e.g. countries that produce a range of products. Putting all of one's eggs in a single basket, as the saying goes, sometimes leads to catastrophes, and, it appears, greater variability as well.

APPENDIX A: CORRECTIONS APPLIED TO TIME-SERIES

Let s_{tuv} be the number of birds of species u counted at route v in year t. The raw total counts $R_{tu} = \sum_{v}^{N_t} s_{tuv}$ contain information about the abundance of species u in year t as well as information about the number N_t and distribution of routes surveyed in year t. The goal is to remove the bias in the counts R_{tu} introduced by variation in the number and distribution of survey routes through time. We do this by replacing each count s_{tuv} for a given species at a given route with the time average $\mu_{uv} = T_v^{-1}\Sigma_t s_{tuv}$ for that route and species, where T_v is the number of years that route v was surveyed. We then construct new, surrogate time-series

$$M_{tu} = \sum_{v}^{N_t} \mu_{uv}$$

whose variation only reflects changes in the number and distribution of survey routes through time (because the same μ_{uv} is used in each year), and not any real change in abundance. We can then generate a bias-corrected time-series by subtracting these new time-series from the raw totals:

$$S_{tu} = R_{tu} - M_{tu} + \bar{M}_u, \tag{A 1}$$

where $\bar{M}_u$ is the time average of M_{tu} for species u. The advantage of this approach is that survey routes added or removed outside a species range will not influence the corrected total, because these routes will have $\mu_{uv} = 0$.

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