

the appearance of genuine long-term trends. Furthermore, although there is a good correlation between the CBC index and estimated true densities<sup>2,4</sup> (suggesting that only a small part of the variance in the index values results from sampling error), in some species correlation between the index and estimated true densities is apparently weak. The important question is whether random variation of reasonable magnitudes could produce an increase in variance of the magnitude demonstrated by Pimm and Redfearn. I have carried out simple simulations that suggest that it could.

Because there is good evidence for systematic changes in the populations of British birds<sup>4</sup>, I do not believe that Pimm and Redfearn's conclusions should be dismissed, but merely that they are less well-founded than appeared at first sight.

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SIR—I suggest that there is an alternative explanation for Pimm and Redfearn's<sup>1</sup> observations that is consistent with a white-noise hypothesis of environmental variation in terrestrial environments<sup>5</sup>—at least over the timescales they examined (up to 30 years).

The phenomenon, the standard deviation of the logarithm of the annual density (SDL) increasing with the census period, may result from autocorrelation between densities in adjacent years; they will be more similar than years that are far apart. In the redshift model the populations are being driven by an autocorrelated environment. An alternative explanation is that the observed autocorrelation results from the population dynamics of the animals themselves.

The density in year *t* may be similar to that in *t*-1 because the same animals may be present at both times, or because it depends on the number of breeders available in the previous year. The environmental influences can then be uncorrelated white noise, and the same pattern of SDL increasing with census length will appear. The autocorrelation is thus present despite the environment, not because of it. Such a model, density depending only on the number in the previous year plus a random environmental perturbation, is called a first-order autoregressive (AR1), or Markov, process<sup>6</sup>. Such autoregressive models can give redshifted spectra<sup>7</sup> for the populations' series even though the environmental driving variables are white noise. Indeed, any relatively smooth time series will have its power concentrated at the lower end of the spectrum<sup>8</sup>.

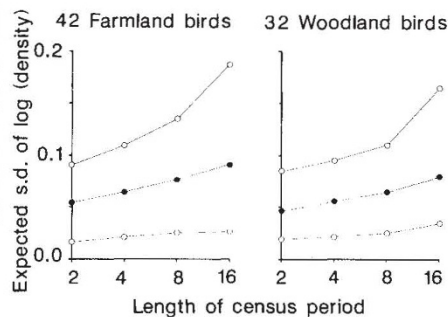
If the data do follow an AR1 model, then the expected value of the SDL from a short census period will underestimate the

true variability of the population. But as the census period increases, the expected value of the sample SDL will asymptotically approach the true value. Thus Pimm and Redfearn's effect could be the result of small sample bias in the estimator of the true, constant, SDL. The expected value of the SDL, (*E*[*s*]) is given by,

$$(E[s])^2 = \frac{N}{N-1} \sigma^2 \left\{ 1 - \frac{1}{N} - \frac{2}{N} \left[ \sum_{t=1}^{N-1} \left( 1 - \frac{t}{N} \right) \rho^t \right] \right\}$$

(ref. 9) where  $\sigma$  is the true SDL,  $\rho$  the autocorrelation and *N* the number of years in the census.

To determine whether this small sample bias could explain Pimm and Redfearn's results, the autocorrelations were calculated for the farm and woodland bird populations used in their paper, and then corrected for their own small sample bias<sup>9</sup>. Though the data sequence is too short for



Expected SDL if the populations follow an AR1 model, calculated using the equation given, against the length of the census period. The mean, maximum and minimum SDLs calculated over the species are plotted at each census length.

formal investigation, the partial autocorrelation structure of most of the species was consistent with an AR1 model, though in some species there was support for a higher-order model. There was evidence for long-term trends (non-stationarity) in only six of the 74 populations studied. Using the SDL's for the 16 years as a starting point, the SDLs for 2-, 4- and 8-year censuses were calculated for each species using the above equation. The mean, maximum and minimum for each census length are displayed in the figure, they are similar in shape and magnitude to those of Pimm and Redfearn. Had higher-order models been fitted, the curves would be even steeper, but the quality of the data does not justify a more complex model.

Thus, the available data do not allow us to distinguish between the white and red-noise hypotheses of environmental variation.

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PIMM AND REDFEARN REPLY—Not surprisingly, there are many explanations for the increase in temporal population variability over progressively longer time spans<sup>1</sup>. These explanations are not mutually exclusive, and no explanation has logical priority. Whatever the explanations, the implications for community dynamics remain.

Part of the increase, for some species, can be explained by certain sampling problems, but this cannot apply to all the data in which increases are found. A population-level explanation comes from the consequences of a population's dependence on the densities of previous years. Long-lived species or those with density-dependent dynamics will show strong autocorrelations between years.

There are also community-level explanations. There is abundant evidence that each species' dynamics depends on many other species in the community. Simple, multi-species population models can produce chaotic dynamics with redshifted spectra<sup>10</sup>. An ecosystem-level explanation is that abiotic variables determine densities both directly and indirectly by altering species' access to resources and their escape from enemies. Clark's<sup>11</sup> investigation of the frequencies of fires is just one independent demonstration of how constantly changing physical processes drive terrestrial populations.

A single explanation for the increase in variability is unlikely. It is found in populations with complex cyclical changes in density, probably caused by interspecific interactions. The increase is also found in populations of long-lived birds and mammals (which have high year-to-year autocorrelations). But there is also more variability over 32 years than 16 years in a newly analysed set of seven moth<sup>12</sup> and three diatom species<sup>13</sup>. These species are short-lived; for insects demonstrations of density-dependent processes are few.

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