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The Temporal Variability of Animal Abundances: Measures, Methods and Patterns

Kevin J. Gaston and Brian H. McArdle

Phil. Trans. R. Soc. Lond. B 1994 **345**, 335-358
doi: 10.1098/rstb.1994.0114

The temporal variability of animal abundances: measures, methods and patterns

KEVIN J. GASTON[1] AND BRIAN H. McARDLE[2]

[1]*Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
[2]*Biostatistics Unit, School of Biological Sciences, University of Auckland, Private Bag, Auckland, New Zealand*

CONTENTS

	PAGE
1. Introduction	336
2. What is variability?	336
3. Which variability?	336
(*a*) Population size or density?	336
(*b*) Which population size or density?	337
(*c*) A model	337
(*d*) Structural versus sampling zeros	337
(*e*) Including or excluding sampling variability	337
4. Measures of variability	338
(*a*) Measures that include sampling error	339
(*b*) Excluding sampling error	341
5. Sampling for variability	341
(*a*) Sampling considerations for variability of density	341
(*b*) Sample size	341
(*c*) Sampling properties of variances	342
(*d*) Confidence intervals	342
(*e*) Sampling unit size	342
(*f*) Frequency of sampling	343
(*g*) Extent of sampling universe	343
(*h*) Hierarchical sampling	344
6. Methods of analysing variability	344
(*a*) Types of data for variance–mean relationships	344
(*b*) Data requirements	345
(*c*) Describing the variance–mean relationship	345
(*d*) Making comparisons between species	346
(*e*) Inter- and trans-specific variability–mean plots	347
(*f*) Variance component estimation by Analysis of Variance	347
(*g*) Variance component estimation in log–linear models	348
(*h*) Detecting patterns within time series	348
7. Patterns in the temporal variability of abundances	349
(*a*) Intrinsic factors	349
(*b*) Extrinsic factors	352
(*c*) Consequences	353
8. Conclusions	354
References	354

SUMMARY

From first principles, the temporal variability of a time series of abundances can be defined as the average deviation of values from a mean value on a proportional scale. In this paper we review: (i) the different kinds of temporal variability; (ii) the different ways in which it can be measured; (iii) the design of appropriate sampling schemes; (iv) methods of analysing variability; and (v) patterns in temporal variability. We emphasize that some commonly applied measures are not appropriate, that several do not measure the desired feature of time series, and the importance of considerations of trend and sampling error. A number of suggestions are made for the improvement of the basis for comparative analyses of levels of variability, and some of the potential pitfalls are identified. Given the serious faults in many previous analyses of ecological patterns in the temporal variability of animal abundances, emphasis is laid on the theoretical basis for different patterns, and hence a set of hypotheses for testing is generated.

Phil. Trans. R. Soc. Lond. B (1994) **345,** 335–358
Printed in Great Britain

1. INTRODUCTION

The abundances of animals fluctuate through time. These dynamics, as well as having inherent interest, impinge upon the study of many areas of population and community biology, both theoretical and applied. An ability to derive summary statistics which broadly describe them would thus seem highly desirable. Indeed, under the banner of indices of variability in abundances, a variety of such statistics have both been proposed and employed. It is apparent, however, that not all of these indices can measure the same thing, and not all seem to measure the abundance characteristic that was intended. Moreover, there has been a growing realization that many indices and/or the ways in which they have been used have led to results being reported which may be spurious, artefactual, misleading, or lacking in the generality that has been supposed. In this paper we consider what is the temporal variability of abundances in a time series, and the different forms it can take. We review how it can be measured, and the different methods of sampling for and of analysing temporal variability. Finally, we review various ecological patterns in levels of variability.

2. WHAT IS VARIABILITY?

As with so many other areas of science the measurement of the variability of animal abundances has been complicated by problems of definition (see Pimm 1984*a* and references therein). The intuitive concept of the variability of abundances is often difficult to crystallize and without a definition it is impossible to look for an appropriate measure. In consequence, researchers and statisticians have tended to apply whatever statistics can be measured conveniently rather than use a definition to design an appropriate statistic. They have tended to work from the data towards the concept, rather than from the concept towards the data.

Any definition of variability should start from first principles and be embedded firmly in the intuitive understanding of the variability of abundances which ecologists seem to share. Of course, to some extent the definition will depend on what you want to use it for. There are two main purposes. One is purely statistical: the variability is needed not for itself but to aid in the achievement of some statistical goal, to calculate confidence intervals on a mean, perform a significance test, or design a sampling program to describe mean abundances. However, increasingly, the measure of variability is needed as a description of the behaviour of animal abundances, to provide ecological insights. In both cases the measure will usually be an estimate of one of the standard variability statistics: the variance or standard deviation. However, in the first case the scale used will be determined by the statistical needs of the moment and need not necessarily have biological relevance (the scale defined by the arcsin ($\sqrt{p}$) transformation comes to mind). When the variability is to have biological meaning the choice of scale is crucial. Most ecologists seem to agree that any measure of variability should measure proportional change. This is based on the reasonable assertion that when considering population variation a change in density from 0.01 to 0.1 is biologically equivalent to a change from 10 000 to 100 000 (Williams 1937; Williamson 1972; Whittaker 1975).

In this paper we regard the temporal variability of abundances as the average deviation of a time series of abundances from an average value on a proportional scale.

One reason that ecologists like a proportional scale is that it confers on a measure of variability a degree of independence from the mean abundance. If two populations have identical sequences of growth rates then the variabilities estimated from the resulting time series should be the same, regardless of the abundances. In this sense the ecological concept of variability implies an independence from the mean abundance. Of course there is no reason why a population need have underlying dynamics which are independent of the mean abundance (for example density dependence may operate), so within a species any measure of variability we use may differ between mean abundances, and this should imply the dynamics are different at different mean abundances. This distinction is an important source of confusion within the literature as to the interpretation of 'mean dependence'. A good measure of variability will be independent of the mean abundance if the dynamics are the same, but will not be independent if the dynamics change with mean abundance (as they often do, see § 6). Hurlbert (1990) noted this same confusion in a spatial context.

3. WHICH VARIABILITY?

Variabilities can be calculated for many different kinds of data. The choices which are made determine what it is that those variabilities measure. Here we identify some of the most important distinctions.

(*a*) *Population size or density?*

It is crucial at the outset of any study to determine explicitly the critical sampling unit for which the variability of abundances is to be calculated. Is the sampling unit a population so that the variability of the size of the population is being measured, or is it a unit of space (a site, a quadrat) so that it is the variability of population density that is being described? The major difference between the two is that for temporal variability the spatial extent of the population being studied may vary from time period to time period. Density of course will tend to be measured on sampling units of constant area, or at least will be corrected to constant area before the variability is estimated (bearing in mind that the density of a species commonly declines with the size of the area over which that density is measured, e.g. Schonewald-Cox & Buechner 1991; Schonewald-Cox *et al.* 1991). Recognition of the difference between studying population size and population density is

important because it is, for example, quite possible to have a population that varies widely in size over time but whose density remains constant (McArdle & Gaston 1993). The areal extent of the population varies to accommodate any change in animal numbers.

The distinction between population size and density is not always as clear cut as it might at first appear (McArdle & Gaston 1993). Populations vary from being completely closed and discrete to being completely open and having no recognizable natural boundaries. In the latter case there is no local population whose size can be measured and one is reduced to measuring density rather than population size. For example, measuring the variability of the numbers of aphids in a field is effectively measuring the density of the animals. It is stretching the definition to call such open systems populations.

The vast majority of available data for animal abundances are concerned with densities, perhaps because such information is much more readily collected. One consequence has been that most studies of variability in the abundances of animals have analysed density not population size data.

Some workers, instead of measuring density directly are forced to use relative indices (e.g. trap returns, nest-box occupancy). As Xia & Boonstra (1992) point out if these indices have a nonlinear relationship with absolute density (as many of them will), measures of variability can be seriously biased.

(*b*) *Which population size or density?*

The variability of a population (size or density) will be markedly affected by the time of year, and the way in which, it is sampled. This problem can be seen at its clearest in species with non-overlapping generations. The variability we measure by sampling at the time of peak abundance is likely to be different to that we obtain from sampling at any other time. Similarly, sampling by summing over the entire generation is likely to produce a different result to sampling at a point in time. Any species with seasonal recruitment or mortality will suffer from the same problems. It is important that a worker define quite clearly which population is being studied, so that like may be compared with like.

(*c*) *A model*

We suggest that the following model approximates many field situations. A population with unknown size or density π_t is measured at time t. A single estimate is taken giving a value N_t. This has a population mean (expected value) of π_t, but comes from an unknown distribution. The parameter π_t varies through time. On occasion the population will become extinct so there will be no population and therefore no density or size: π_t is undefined. This is an important assertion. As other workers have noted (Pimm *et al.* 1988; Schoener & Spiller 1992) if we are primarily interested in the variability of a population, then periods when it is not there can tell us nothing about its variability.

(*d*) *Structural versus sampling zeros*

This model leads us to a theoretical distinction between two types of zeros. There are sampling zeros, where the population is present ($\pi_t > 0$), but was not present in the sample, and structural zeros where the population is really extinct (π_t is undefined). To measure the variability of a population, we need to incorporate sampling zeros but exclude structural zeros. If we leave in all the zeros we are measuring the variability not of the population (size or density) but of the number of individuals per sample. Our sampling unit is no longer the population but the area sampled (the quadrat or transect), and the variability we are measuring is of the time series, which if there are structural zeros is a property of the area sampled not of the population (Gaston & McArdle 1993; McArdle & Gaston 1993). Of course, if there are no structural zeros the time series describes both. As we shall see below the ability to distinguish between the two types of zero is crucial. Unfortunately, in most cases it will be difficult to do so.

Even if an attempt has been made to count the entire population, it will often be impossible to state with any certainty when the population has gone extinct (McArdle 1990). Failure to find any animals does not always mean that there may not be one or more still present. This is especially true for organisms with resting or inconspicuous stages (e.g. eggs or pupae) or ones that live in structurally complex environments. It will seldom be possible to state with certainty that a population has gone extinct until a number of attempts to locate it have been made over an extended period of time (e.g. Kuno 1991). It is therefore often difficult to distinguish between a censused zero that means that the population is extinct (structural zeros) and zeros that are due to sampling error when the population is really present (sampling zeros). As we mentioned earlier this is an important distinction. If you are measuring the variability of a population then structural zeros must be excluded. Including them will inflate most measures of variability (McArdle & Gaston 1992). This effect will be particularly large with species whose local populations suffer cycles of extinction and recolonization. Excluding sampling zeros in the mistaken belief that they are structural will reduce most measures of variability leading to an underestimate of the true population variability.

(*e*) *Including or excluding sampling variability*

Returning to our simple model, if we measure the variability of the N_t values we are confounding sampling error with the variability of the densities (i.e. the variability of π_t). For any given time-series there are two situations, that where it is possible to estimate the sampling error and so extract an estimate of the variability of π_t, and that where only the

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Table 1. *Sampling estimators of measures of variability which have been proposed, and in most instances applied*
(CV = coefficient of variation $[\mathrm{SD}(N)/\bar{N}]$, GM = geometric mean, n = sampling units, SD = standard deviation. Where the original paper used the variance we have referred instead to the SD as this is a more easily interpreted scale.)

(i) *arithmetic*		
(1) $\mathrm{SD}(N_{t+1} - N_t)$		Leigh (1983)
(2) $\mathrm{SD}(N)$	standard deviation of untransformed values	Tracy & George (1992)
(3) $\mathrm{SD}(R)$	variance of net reproduction (net reproduction $R = N_{t+1}/N_t$)	den Boer (1981)
(ii) *proportional*		
including sampling error		
total variability		
(4) $\mathrm{SD}[\log(N)]$	standard deviation of log-transformed values	Williamson (1972, 1984), Connell & Sousa (1983)
(5) $\mathrm{antilog}\{\mathrm{SD}[\log(N)]\}$	'coefficient of fluctuation'	Whittaker (1975), Holmes *et al.* (1986)
(6) $\mathrm{antilog}\{3 \cdot \mathrm{SD}[\log(N)]\}$		Williamson (1972, 1984)
(7) $\mathrm{SD}[\log(N+i)]$		Joern & Pruess (1986)
(8) $\mathrm{antilog}\{3 \cdot \mathrm{SD}[\sinh^{-1}(N)]\}$		Williamson (1981), Samways (1990)
(9) $\ln\{\mathrm{var}[\ln(N)]\}$	'stability index'	Wolda (1983*a*, 1992)
(10) $\mathrm{CV}(N)$	coefficient of variation of untransformed values	Brewer (1963)
(11) $\mathrm{V_p} = \mathrm{CV}^2/n^2$		Soberón & Loevinsohn (1987)
(12) $N_{\max}/N_{\min+1}$	proportional range	Glazier (1986)
(13) $\log(N_{\max}/N_{\min})$	logarithmic range	Hassell *et al.* (1976), den Boer (1981)
(14) $\sqrt{\{\mathrm{mean}[N_t/\bar{N} - N_{t+1}/\bar{N}]^2\}}$		Spitzer & Lepš (1988)
(15) $\mathrm{mean}[\log(R)]$	mean reproductive rate	Taylor & Woiwod (1980)
average size of change		
(16) $\mathrm{mean}\lvert\log(R)\rvert$		Pollard (1984)
(17) $\sqrt{\mathrm{mean}\{[\log(R)]^2\}}$		Spitzer & Lepš (1988)
variation around linear trend		
(18) $\mathrm{SD}[\log(R)]$	'annual variability' detrended variability	Wolda (1978, 1983*c*)
(19) $\mathrm{CV}(R)$		this study
excluding sampling error		
(20) $\sqrt{\{[\mathrm{var}(N) - \bar{N}]/\bar{N}^2\}}$	'proportionate variability'	Samways (1990)
$\mathrm{CV}^2(\lambda)$	corrected CV	B. H. McArdle & K. J. Gaston, unpubl.
(21) $[\mathrm{var}(N) - \bar{N}]/\bar{N}^2 + 1$	Morisita's index Lloyd's Index	Morisita (1962), Lloyd (1967)
(22) $\sqrt{(\mathrm{trigamma}\{[\mathrm{var}(N) - \bar{N}]/\bar{N}^2\})}$	SD $[\log(\lambda)]$ Negative Binomial	B. H. McArdle & K. J. Gaston, unpubl.
(23) $\sqrt{(\log\{[\mathrm{var}(N) - \bar{N}]/\bar{N}^2 + 1\})}$	SD $[\log(\lambda)]$ Poisson log–normal	B. H. McArdle & K. J. Gaston, unpubl.

variability of N_t is estimable. The variability of N_t will be larger than that of π_t.

4. MEASURES OF VARIABILITY

A large number of measures of 'temporal variability' have been proposed for animal abundances (table 1; measures will subsequently be referred to by the numbers given to them in the table). Of these we will consider only those that operate on a proportional scale. Only these are likely to conform to the ecologist's concept of variability. Thus in figure 1 populations A, B, and C should have the same value for the measure of variability, as population A is varying from 10 to 20, B from 1 to 2, and C from 0.1 to 0.2. Because most workers prefer to use the standard statistical measures of variability, i.e. variance or standard deviation (s.d.), the important question is which scale to work on. Apart from the linear scale three others are commonly used: the $\log(N)$, the $\log(N+1)$, and N/mean (the standard deviation of which is the coefficient of variation, CV). It is clear from figure 1 that while the standard deviation on the logarithmic scale and N/mean scales do indeed provide a constant measure of variability, there is a bias in $\log(N+1)$ (mentioned in McArdle *et al.* 1990). This bias is present whenever there are low densities, regardless of the shape of the variance–mean relationship. It has also been noted by Anscombe (1948), Williams (1937, 1964) and by Williamson (reported in Samways 1990).

In this section we shall concern ourselves with single time series of counts, where the population size or density estimated at one time is unreplicated, i.e. has no direct estimate of sampling error. It is therefore convenient to separate out those measures that ignore the existence of sampling error, and those that attempt to estimate the variability of the underlying densities by assuming a special case of the simple sampling model described earlier.

Many studies consist of a single count of animals estimating the density at each time period. In many of these situations it is reasonable to assume that the number observed at each time period (N_t) is a sample

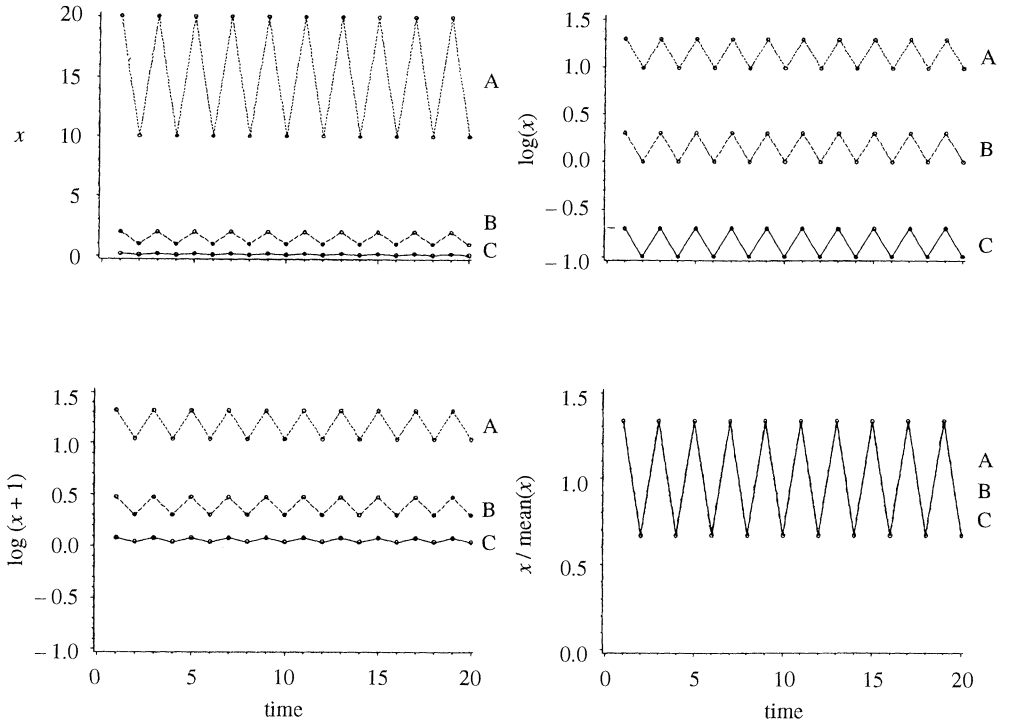

Figure 1. Three artificial population density time series plotted on four different scales. (*a*) Linear scale: SD population A = 5.12, B = 0.512, and C = 0.0512. (*b*) Logarithmic (base 10) scale: SD population A = 0.154, B = 0.154, and C = 0.154; logarithmic (base e) scale: SD = 0.355. (*c*) Logarithmic $(N+1)$ scale: SD population A = 0.144, B = 0.090, and C = 0.019. (*d*) N proportional to mean (for CV): SD population (= CV) A = 0.342, B = 0.342, and C = 0.342. Note the similarity of the CV to the SD[ln (N)].

from a Poisson distribution with mean density λ_t which themselves come from an unknown distribution. The distribution of N_t values will therefore be over-dispersed (variance greater than the mean), we therefore call this the over-dispersed Poisson model. If this model is appropriate then there are measures that can estimate SD[log (λ)] instead of SD[log (N)].

In addition to sampling error, trends in time series also present a problem. There are three obvious ways of measuring variability in the presence of trend. What they describe is best seen in relation to figure 2.

1. Measure overall variability including trend, a measure of the changes in abundance. In figure 2 such a measure would distinguish between the stationary (A) and trended situations (B and C), but as the series lengthened it would not distinguish between B and C.

2. Measure the magnitude of changes in abundance regardless of direction. This would not distinguish between the stationary process (A) and the simple trend (B) because the change over a time period is the same in both, only the direction varies. It would, however, distinguish C because some of the changes are large (combining trend and oscillation).

3. Measure variability of the abundance around the trend, removing the trend in some way, to provide a measure of the variability of the underlying dynamics (hereafter distinguished as a measure of the 'variability of dynamics'). Here the simple trend B is recognized as having no variability, while the oscillations in A and C would be seen as equivalent.

Which of these three approaches a worker would use would obviously depend on the problem being studied. They address very different types of variability and cannot be interpreted in the same way.

(*a*) *Measures that include sampling error*

(i) *Total variability*

The measure most workers would like to use is probably SD[log (N)], the measure they commonly use is SD[log $(N+1)$], and the measure we think they ought normally to use is the coefficient of variation [CV(N)]. Figure 1 clearly shows that SD[log (N)] and CV(N) are truly on proportionate scales. SD[log $(N+1)$] is not; populations that have the same proportional changes could have different values of SD[log $(N+1)$]. All statistics that rely on adding a

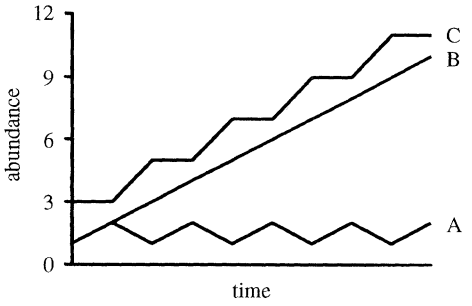

Figure 2. Three artificial time series of population densities. A, unit oscillations with no trend; B, unit trend with no oscillations; and C, unit trend with unit oscillation superimposed.

constant to remove zeros before a logarithmic transformation will have a similar bias. We suggest that SD[log $(N+1)$] never be used as a measure of variability as it does not measure what ecologists understand as the variability of animal abundance. The $\sinh^{-1}(N^{1/2})$ transformation (measure (8)) has been shown to have similar problems (McArdle *et al.* 1990).

Given SD[log (N)] and CV(N), which should we chose? If there are no zeros in the data then SD[log (N)] is probably the more natural (Williams 1937; Williamson 1972, 1984). In fact, the results of any comparative analysis should be qualitatively the same whichever is used (provided there are no zeros) because the two tend to give very similar values. The reasons for this can be appreciated by examining them more closely. SD[log (N)] can be re-expressed as SD[log (N/GM)], where GM is the geometric mean of the abundances. CV can be re-expressed as SD(N/AM) where AM is the arithmetic mean. Both are measuring variation proportional to a mean value, but SD[log (N)] does it on a logarithmic scale, CV on a linear one. If natural logarithms are used then when the variability is relatively small (e.g. CV $< 30\%$) the difference in scales is negligible (Lewontin 1966), and both statistics give near identical values. An alternative approach that argues for the similarity of SD[log (N)] and CV is the fact, relatively well known among statisticians, that if the log (N) values are not available then CV$^2(N)$ is a distribution-free estimator of $\{\mathrm{SD}[\log_e(N)]\}^2$, using the delta method (Seber 1982). In practice, the similarity between these two measures means that if two populations have the same values of CV(N) then the values of SD[log (N)] will nearly always also be very similar, and if the values of CV(N) are different then those of SD[log (N)] will also be different.

Using a different approach, Soberón & Loevinsohn (1987) derived the variance (V_p) of time series after counts had been converted to proportions of the total count (measure (11)). They are therefore also working explicitly on a proportional scale. However, they showed that V_p is simply CV$^2(N)/n^2$, where n is the number of time periods. It therefore contains the same information as CV, but its value depends explicitly on the length of the time series.

Although SD[log (N)] is a logical statistical measure of what ecologists would call variability, as a number it is not easily interpreted. Williamson (1972, 1984) and Whittaker (1975) have suggested that there are two more accessible variants (measures (5) & (6)). The values of log (N) tend to be approximately normally distributed, 68% of the observations of a normal distribution are expected to lie within the interval mean ± 1 SD and 90% within mean ± 1.5 SD. If 68% is taken as an arbitrary estimate of 'commonly' (Whittaker 1975) or 90% as an estimate of the range (Williamson 1972, 1984), this allows statements such as 'the densities in different years are mostly not more than 18% above or below the mean' (Whittaker 1975), and 'the population highs are about 10 times the population lows' (Williamson 1972, 1984).

An alternative approach is to measure the proportional range directly, $N_{\max}/N_{\min}$. Unfortunately, the minimum value of N is often 0, leaving this measure undefined. One expedient, applied by Glazier (1986), is to use the smallest non-zero value $(N_{\min+1})$ instead of $N_{\min}$ (measure (12)). The range statistic but on the logarithmic scale (measure (13)) has also been applied. All three of these measures though intuitively appealing and easily interpreted suffer, as the range always does, from an extreme sensitivity to sampling error. We would not recommend them for general use.

Some authors have suggested that as it is the dynamics that are of interest, attention should be concentrated not on the deviations from the mean, but on the differences between successive time periods. This has led to a family of measures based on $R = N_{t+1}/N_t$, or $D = N_{t+1} - N_t$. This approach has the potential of addressing the problem of trend. Spitzer and Lepš (1988) suggested measure (14) based on D standardized by the arithmetic mean. They argued that this measure was trend free, unfortunately it is profoundly affected by trend, and effectively acts like CV(N) though with very different values, so there seems to be no reason to use it.

Measure (15) is simply a measure of the trend itself. As the average change (on a logarithmic scale) it will be zero if there is no trend and have a large value in the presence of a strong, consistent, monotonic, trend. It is the geometric mean proportional change expressed on a logarithmic scale. An arithmetic one would be more interpretable as it would allow statements like 'the population density is on average increasing by 15% per time period'.

(ii) *Measuring average size of change*

Measures (16) and (17) are essentially measuring the same thing, the average magnitude of change (irrespective of direction). As such they are clearly not trend-free. In figure 2 they cannot, for example, distinguish between the stationary oscillations of A and the simple trend of B, the changes are of the same magnitude. Measure (17), the root mean square difference in logarithms will be equal to $\{2(1-\rho)\,\mathrm{var}[\log(N)]\}^{1/2}$, as noted by Williamson (1984), where ρ is the autocorrelation coefficient, but only if the process is stationary, trend free.

(iii) *Measuring fluctuations around trend*

We have found only two measures that appear to measure fluctuations around a consistent linear trend. They are SD[log (R)] and its estimate CV(R). Because neither of these measures can be used when there are zeros in the data there seems little point in using CV(R), SD[log (R)] seems more natural. SD[log (R)] will be equal to $\{2(1-\rho)\,\mathrm{var}[\log(N)]\}^{1/2}$, as noted by Williamson (1984), where ρ is the autocorrelation coefficient. Both are measures of the average deviations of proportional change around the average proportional change. They can be thought of as attempting to estimate the variability of the multiplication rate around a consistent trend. Of course, if

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

the underlying trend is markedly nonlinear, then these measures will be inflated, a more formal method of trend removal would have to be tried (Chatfield 1984).

One feature of this measure is that it is likely to be more sensitive to the frequency of sampling than SD[log (*N*)]. Because it is based on the ratio of consecutive samples, if these are close together in time relative to the turnover rate of the organism studied then the ratio *R* is likely to be close to one (i.e. small SD[log (*R*)]). The further apart the samples are, the larger SD[log (*R*)] is likely to be. This is of course a reflection of the autocorrelation effect mentioned above (SD[log (*R*)] = $\{2(1-\rho)\,\mathrm{var}\,[\log(N)]\}^{1/2}$). The autocorrelation coefficient will tend to be greater for samples that are close together relative to the rate of turnover in the individuals.

(*b*) *Excluding sampling error*

All the above measures are commonly used on data that include sampling error, and this can often influence the behaviour of their relationship with mean abundance (see §6). Many, if not most, workers would rather have the variability of the underlying densities uncontaminated by sampling error. We discuss below methods that can be appropriate if the samples are replicated at each sampling period, so direct, empirical, estimates of sampling error can be derived. However, when this has not been done and single counts are all that are available, then it may be possible to use a measure of variability that estimates the uncontaminated variability (B. H. McArdle & K. J. Gaston, unpublished results). If the over-dispersed Poisson sampling model is appropriate for describing the sampling situation, then three such measures can be used.

Since calculating SD[log (λ)] is impossible without making certain restrictive assumptions about the distribution of λ_t, it is probably more sensible to use CV(λ) instead. This is simple. Regardless of the distribution of λ_t, if the augmented Poisson distribution holds, $\mathrm{CV}^2(\lambda)$ has the formula:

$$\frac{\sigma_N^2 - \mu_N}{\mu_N^2}. \qquad \text{measure (20)}$$

As we observed earlier CV(λ) is a distribution-free estimate of SD[log (λ)]. Expressed as a percentage CV this is the Charlier coefficient used in a spatial context by Beall (1935) and Cole (1946; see also Green 1966). With the addition of 1, $\mathrm{CV}^2(\lambda)$ becomes equivalent to Lloyd's index of patchiness and Morisita's index (measure (21); Lloyd 1967; Morisita 1962; Hurlbert 1990).

This measure has a useful property that may aid interpretation. As Pielou (1969) demonstrates in a spatial context, it remains unchanged under random thinning. If the average density is reduced over all sites by strictly random mortality, then the variability of the density CV(λ) remains unchanged. This supports the assertion made at the beginning of this paper that CV measures changes in population on an ecologically appropriate scale. This interpretation can be generalized to temporal variability, in which case we can assert that CV(λ_t) will be constant over all densities if mortality (and birth) processes are independent of density. This then allows us to suggest that slopes of the CV(λ_t)–mean relationship will be negative if density-dependent population dynamics are involved, provided the carrying capacity is relatively constant. We must emphasize that at present this does not allow us to infer density dependence from a negative slope, there may be other, density-independent, dynamics that can produce the same pattern.

If the distribution of N_t can be thought of as negative binomial, then the distribution of λ_t is gamma and SD[log (λ)] is $[\mathrm{trigamma}(\alpha)]^{1/2}$ (measure (22); Johnson & Kotz 1970) where α is $1/\mathrm{CV}^2(\lambda)$, i.e. the reciprocal of the CV^2 of the gamma distribution of λ_t. $\mathrm{CV}^2(\lambda)$ is measure (20).

If the distribution of N_t is assumed to be Poisson log-normal (Cassie 1960), then SD[log (λ)] is:

$$\sqrt{\log\left(\frac{\sigma_N^2 - \mu_N}{\mu_N^2} + 1\right)} = \sqrt{\log\left(\mathrm{CV}^2(N) - \frac{1}{\mu_N} + 1\right)}. \qquad \text{measure (23)}$$

5. SAMPLING FOR VARIABILITY

The most important consideration when designing a sampling regime to measure variability is to realize that a single value of variability will seldom be of much use. As we shall see below, the temporal and spatial variability of many, if not most, species is dependent on the mean abundance. Thus, for any useful generalizations to be made the variance–mean relationship must be characterized. This requires adequate replication not just for the estimation of one mean and one variance, but to provide a series of means and variances that ideally span the range of values found over the animal's spatial distribution.

(*a*) *Sampling considerations for variability of density*

We see as important that the same rigorous statistical criteria be applied to the design of sampling régimes to estimate variance as are employed for the estimation of means in most ecological studies. Any one (or combination) of the standard sampling strategies can be applied for the estimation of variability: random, stratified, hierarchical, or systematic sampling (Cochran 1963; Green 1979; Andrew & Mapstone 1987; McArdle & Blackwell 1989) can all be appropriate.

(*b*) *Sample size*

When sampling for variabilities it is important to remember that variances and standard deviations do not obey the central limit theorem and the precision of standard deviations does not improve with sample size as rapidly as that of means. In figure 3 we show the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

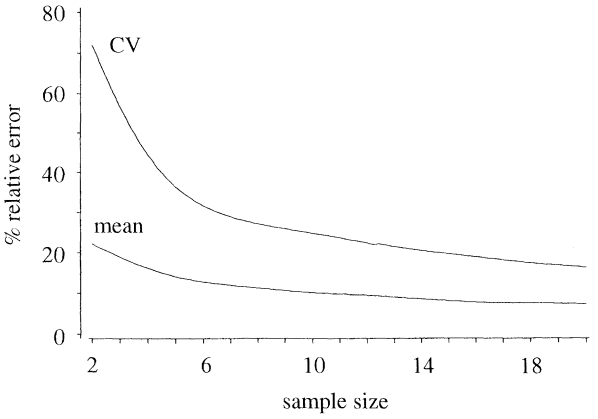

Figure 3. Relationship between percentage relative error on the sample estimators for the mean and CV, against sample size, for a Poisson distribution (mean = variance = 10).

relative error (SE/mean) on mean and the CV, for different sample sizes, calculated from a Poisson distribution (mean = variance = 10). Clearly larger sample sizes are necessary to achieve equivalent precision. This problem is particularly acute for hierarchical or two stage designs. Where there are two or more levels of replication it is crucial to ensure that the variance component of interest has sufficient degrees of freedom, i.e. that replication be concentrated at the appropriate level.

(*c*) *Sampling properties of variances*

Most populations have long-tailed distributions; the higher the mean and the more aggregated the population, the longer the tail. While studies on the shape of temporal distributions are rare, those that exist have tended to show positive skew and long tails. The variance estimate derived from a small sample taken from a long-tailed distribution is nearly always an under-estimate of the true variance. Occasionally a large over-estimate is generated, which keeps the average estimate unbiased. That is, the distribution of sample variances is heavily skewed for an underlying long-tailed distribution (Gower 1987; McArdle *et al.* 1990). This phenomenon is very marked for the negative binomial and related distributions. If we simulate a population with a frequency distribution with mean density 50 and parameter $k = 0.1$, then the true variance is 25 050. Of 1000 samples of size 5 taken from this distribution, 824 estimates of the variance were less than the true value and the median estimate was 1887, less than 8% of the true value. The effect is most marked at small sample sizes. However, using a sample size of 20, 727 of 1000 were still under-estimates, and the median estimate of 9500 was only 38% of the true value. This effect is important for values of k less than 0.5. The CV and trigamma will also be affected by this phenomenon (although not as badly). SD[log (N)], which for temporally contagiously dispersed animals is based on a much less skewed distribution, will be far less so.

It is now well known that variability estimates based on SD[log (N)] tend to increase with the length of the time series (Pimm & Redfearn 1988; McArdle 1989; Crowley & Johnson 1987). We discuss this effect later when considering the extent of the sampling period.

(*d*) *Confidence intervals*

We suggest that the time has now come for people presenting estimates of variability to also provide measures of their reliability. The precision of estimates of variability is nearly always worse than that for the corresponding means. Small standard errors or confidence intervals are achieved only with very large sample sizes (see above). Thus, many, if not most, reported measures of variability actually have such large confidence intervals as to make sensible comparisons virtually impossible.

Putting confidence intervals on measures of variability is often theoretically complex. Computer intensive techniques like the bootstrap or the jacknife for calculating empirical standard errors or confidence intervals are increasingly well established on the ecological scene, and provide a way of getting confidence intervals on variability estimates even when theory cannot provide convenient formulae.

(*e*) *Sampling unit size*

Whichever sampling design is chosen there are some universal considerations. The first of these are the factors that influence the choice of the size of the sampling unit. Perhaps the most important is to choose a unit that minimizes the proportion of zeros in the data set. Even if we are discussing population densities rather than population size, the number of sampling zeros should be reduced as much as possible as these contain very little information about the density of the animals. However, this is not the only consideration.

Ecologists have long been aware that the interaction between sampling unit size (e.g. quadrat size) and the spatial aggregation pattern of a population determines the spatial variability that is observed (e.g. Sawyer 1989; Yamamura 1990). Indeed there are methods of analysis to determine pattern and patch size based on this property (Greig-Smith 1952, 1964; Mead 1974; Usher 1975; Dale & MacIsaac 1989). The effect on temporal variability is less well appreciated (Connell & Sousa 1983; McArdle *et al.* 1990; Thomas 1991). The situation is often confused because not only must the duration of the sampling period be chosen but so must the size of the sampling unit in space. Numbers of animals have to be counted in a finite space, so all the problems associated with spatial sampling have to be confronted.

Comparisons may also be difficult because of the relationship between the size of the sampling unit and the biology of the organism. A recurrent theme of this paper is that there is no single species-specific value of variability, so that between-species comparisons are extremely difficult. One feature of the choice of sampling unit size in space is that if the aggregation patterns of species are different, then the results of

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

comparisons of variability in time at one sampling unit size may be completely reversed at another. Measuring the variability of elephants and aphids using quadrats of the same size would probably not lead to an ecologically informative comparison. Some effort would have to be made to ensure that the sampling units reflected the differences in body size and mobility.

Some sampling methods rely on the accumulation of individuals through time (e.g. light traps, suction traps, pit-fall traps). The choice of the duration of the sampling unit is clearly important. For some of these methods (e.g. many bird counts, visual censusing of fish) increasing the length of the sampling unit increases the probability of counting the same animal twice, or increases the likelihood of turnover in the identities of the individuals present. Correspondingly, too short a time interval and there will be many zeros, with all the problems they entail. In general, the longer the sampling period over which animals are counted the smoother the resulting time series. For example, counting the number of starlings on a bird table for one minute every day will generate a high variability, many zeros and a few larger numbers. Accumulating the count continuously for a year the variability (as opposed to the variances) will, in general, be less.

Lepš (1993) proposes the use of techniques derived for spatial investigations of scale (e.g. Hill 1973) to investigate how temporal variability changes with temporal scale. This can provide much useful information about the dynamics of the study population (e.g. McArdle & Blackwell 1989). However, as McArdle *et al.* (1990) point out, when variability is seen as a fundamental property of a species and is to be compared between species there are many complications. Not the least of these is the necessity of using a biologically comparable scale (e.g. generation time). These techniques are in essence pooling adjacent sampling units and creating units of longer duration. However for comparisons between species the unit over which the counts are integrated must be biologically comparable. Studies that pool counts over different numbers of generations in different species will not generate comparable variabilities.

There may be problems in defining the generation time of a species if it has a complex life-history or multiple reproductive strategies, in particular large variances in generation time are problematic (Lepš 1993). These may be generated either within a cohort (e.g. some proportion of the population enters dormancy, while the rest do not) or between cohorts (e.g. every other cohort overwinters). Generation time as a sensible temporal scale is not always ideal. Nonetheless, we are unable to find a scale that would allow the variability of aphids and elephants to be compared that is not in some way proportional to the lengths of their lives.

When comparing species there may be situations where the scale can be defined relative to the scale of another system. For an agricultural scientist the variability of an insect population might more usefully be measured relative to the growth cycle of a crop rather than the generation time of the species itself. There will be a number of situations where the timescale will be defined by the dynamics of a different species (e.g. prey or crop) than the one whose variability is actually being measured. A related situation is that of the conservationist (and other anthropocentric contexts) where the timescale is defined by the management objectives and not by the biology of the particular species.

(*f*) *Frequency of sampling*

There is confusion between the role of the appropriate scale of sampling in choosing the duration of the period over which to integrate or pool animal counts and the frequency with which the counts should be taken. As we showed above, if counts have to be integrated over a time period, then a generation time or constant fraction thereof could be chosen. However, many authors do not seem to have appreciated that it is not necessary to sample at intervals one generation apart if the generations are overlapping (e.g. Connell & Sousa 1983; McArdle *et al.* 1990). Sampling an elephant population every year will not give very much more information about variability than sampling every ten years or even every complete turnover, but the expected value of measures of total variability will be the same regardless of the frequency. Conversely, measures of the variability of dynamics (i.e. SD[log (R)] will be affected by the frequency of sampling.

(*g*) *Extent of sampling universe*

If replicate sampling units are to be taken at each time period, to allow sampling error to be removed, then similar considerations as pertain to ensuring that the size of sampling units enables appropriate comparisons also apply to the spatial extent of the sampling universe (the statistical population of sampling units whose variability one intends to describe). If we wish to describe the temporal variability of density within a population the sampling design must ensure adequate coverage in time and space. An estimate of the temporal variability of the abundance of aphids in Tsavo national park will usually not be considered usefully comparable on a biological scale with the temporal variability of the abundance of elephants even if the sampling units are scaled appropriately. The extent of Tsavo (the sampling universe) as utilized by aphids is unlikely to be comparable with how elephants use it.

The extent of the temporal sampling universe is also important because of the effects of autocorrelation on estimates of variability. Autocorrelation occurs when abundances that are close together, in time (or in space), are more similar than ones that are far apart. One consequence of autocorrelation is that measured temporal population variabilities tend to increase with the length of a time series (Pimm & Redfearn 1988; McArdle 1989; Hanski 1990; Andrews 1991; Pimm 1991).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

There are three main sources of autocorrelation. The first is external. The environmental conditions driving the dynamics of a population are more similar in sampling units that are close together in time than in ones that are far apart (the 'reddened spectrum'; Williamson 1987; Pimm & Redfearn 1988).

The second source of autocorrelation is internal. When we are measuring temporal variability some animals counted in one census may still be alive in the next, or the number of individuals in one generation may depend on the number of breeders in the previous one (McArdle 1989). All that is required is that the number of animals alive in consecutive time periods be more similar than the numbers in periods that are far apart. Contrary to the suggestions of Pimm & Redfearn (1989; Pimm 1991), this will tend to happen in the absence of density dependence. A random walk, zero density dependence (Pollard *et al.* 1987) has perfect autocorrelation; instant return to a constant equilibrium (perfect density dependence) has zero autocorrelation. Crowley & Johnson (1992) found that a heavily density-dependent model showed little or no increase of variance with series length (i.e. low autocorrelation), while models with weak density dependence showed a marked increase (i.e. high autocorrelation). If, as Pimm & Redfearn (1989) and Pimm (1991) suggest, density dependence is uncommon in insects, autocorrelation may be expected to be high (but see Woiwod & Hanski 1992).

The third source of autocorrelation could be either internally or externally driven. If monotonic trends exist in a time-series then there will be increased autocorrelation, and a natural increase in variability as the series lengthens. Trends are fairly common in nature, most of them being associated with recent human activities (Holmes *et al.* 1986; Holmes & Sherry 1988; Hill & Hagan 1991; Hagan & Johnston 1992; Woiwod & Hanski 1992; Wolda 1992; Pollard & Yates 1993).

As McArdle (1989) explicitly stated, the relationship between variability and the length of a time series is at present equally plausibly explained by the internal and the external explanations for the phenomenon. Several workers have standardized the length of time series as a response to the pattern (e.g. Andrews 1991). Because the degree of autocorrelation, regardless of origin, is likely to be a function of generation time the standardization should be the same number of turnovers not necessarily the same number of time periods.

When studying the temporal variability of abundances one should try at least to minimize the internal sources of autocorrelation. The criterion that the extent of the sampling universe needs to be large enough that the same individuals cannot occur in those sampling units with the greatest separation, in time or in space (one complete turnover; Connell & Sousa 1983; Schoener 1985, 1986) is a step, although an inadequate one, in this direction. Temporal variability based solely on one turnover cannot conceivably give a precise measure of the behaviour of the population. The variability of a population of aphids measured over two consecutive years, for example, will not be reliable.

Internal and external sources of autocorrelation may never be entirely eradicated. To produce an accurate estimate of variability you need a large number of independent observations. If they are autocorrelated you need proportionately more. The sampling universe must thus be large enough to provide sufficient independent replicates or their equivalent in autocorrelated ones. One simple rule of thumb to use is that the effective sample size in an autocorrelated time series is approximately $(1 - r^2)n$, where r is the autocorrelation coefficient and n is the length of the time series.

(*h*) *Hierarchical sampling*

In recent years a desire to investigate the effect of spatial scale on the variability of population densities has led some workers to design multi-level hierarchical sampling schemes (e.g. Kingsford & Choat 1986; McGuinness 1988; McArdle & Blackwell 1989; Jones *et al.* 1990). These can be analysed to identify the scale with the greatest inter-sampling unit variability. Though related in principle to the Greig-Smith type of analysis (Greig-Smith 1952, 1964; Mead 1974; Usher 1975), the sampling is designed to examine nested scales that can extend from quadrats only a few metres apart to regions that are separated by tens or hundreds of kilometres. Though as yet no one seems to have published work using this approach to temporal variation, it is possible (B. H. McArdle and N. M. Coupe, unpublished results). Leaving the problems of the analysis to a later section, the major difficulties of such a design are twofold. First, whereas it may be possible to do within-species comparisons, between-species comparisons are now complicated by effects of scale and extent at every level of the sampling design. Second, it is logistically difficult to ensure sufficient replication at every level in such a way that the resulting measures of variability are sufficiently precise to be useful.

6. METHODS OF ANALYSING VARIABILITY

(*a*) *Types of data for variance–mean relationships*

The interaction between measures of deviations of abundances from the mean and the mean have largely been explored in the context of variance–mean relationships (e.g. Taylor 1961, 1984; Hanski 1982) rather than variability–mean relationships; although the two are obviously closely related (see below).

Soberón & Loevinsohn (1987; see also McArdle *et al.* 1990) distinguish three different kinds of variance–mean relationships. These differ in the derivation of variances and means: (i) spatial sampling, temporal plotting: each data point represents the mean and variance across sites at a given time; (ii) spatial sampling, spatial plotting: each data point represents the mean and variance across sites in a given place; and (iii) temporal sampling, spatial plotting: each data point represents a mean and variance across time at a given site. We suggest adding a fourth: (vi) temporal sampling, temporal plotting: each

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

data point represents the mean and variance across a different time period for the same site (e.g. the variability within a time period say a month is investigated by plotting many months). In the context of the temporal variability of abundances it is the third of these which is primarily of interest.

The bulk of the literature concerned with the description of temporal variance–mean relationships has addressed intra-specific relationships. That is, all means and variances are measured for the same individual species (e.g. Taylor & Woiwod 1980; Hanski 1982; McArdle *et al.* 1990). However, inter-specific and trans-specific plots have also been documented and, in some instances, explored. In inter-specific plots each data point represents the mean and variance in the temporal abundance of a particular species, but each species appears only once (e.g. Hanski 1982; Wolda 1983*a*; Holmes *et al.* 1986; similarly constructed variability–mean plots are documented by, for example, Wolda (1983*a*); Wolda & Roubik (1986); Samways (1990)). In trans-specific plots each data point represents the mean and variance in the temporal abundance of a particular species, but although data points for many species may be plotted some species will be represented more than once. Inter-specific and trans-specific variance–mean relationships are difficult to interpret, confounded as they are with the intra-specific relationships. We discuss them in more detail later.

Finally, we note the existence of analyses of temporal variabilities in the summed abundances of several species, particularly with respect to questions of the temporal stability of different environments (e.g. Järvinen 1979; Wolda 1978; Wolda & Galindo 1981; DeSante 1983; Woolhouse & Harmsen 1987; Virkkala 1989; Bethke 1993; Johansson *et al.* 1993). These essentially lie beyond the scope of this paper, although there may be similarities in appropriate methodological and analytical techniques.

(*b*) *Data requirements*

Various criteria have been suggested which should preferably be met if the fit of descriptive models of the variance–mean relationship is to be determined. These include that the samples (counts) on which a variance is based should number more than 15, that there should be more than five variance–mean pairs, and that the range of abundances should be as large as possible with ideally at least two orders of magnitude being encompassed (Taylor *et al.* 1988; Perry & Woiwod 1992). If the range of abundances are not large enough there can be problems with the reliability of the fitted variance–mean relationship (Downing 1986; Hanski 1987; Hanski & Tiainen 1989).

Titmus (1983) showed that the shape of the spatial variance–mean relationship was markedly affected by differences in sampling efficiency. This effect might well also influence temporal variance–mean relationships. Certainly, if the efficiency is correlated with the mean density (as for example with density indices based on trap catches), then the variance–mean relationship could be quite misleading.

(*c*) *Describing the variance–mean relationship*

There has been a large literature over the years describing and analysing the relationship between temporal variance and mean abundance. The chief characteristic on which most workers agree is that log (variance) and log (mean) are linearly related when the means are above some cut-off value. Depending on the way in which data were collected the relationship can become nonlinear at low densities, a phenomenon noted by many workers, and usually due to sampling error (otherwise known as integer effects, graphically illustrated by Taylor & Woiwod (1982); Taylor (1984, 1986)).

Less commonly, the density at each time period is estimated from the average of replicate counts, so there are no integer effects. In this case the limited information so far available seems to suggest that linearity is preserved even at low densities (B. H. McArdle, unpublished results).

A number of models have been used to describe intra-specific variance–mean relationships. These include: (i) Taylor's power function, $\sigma^2 = a\mu^b$ (Taylor 1961); (ii) the quadratic function, $\sigma^2 = a_1\mu + a_2\mu^2$ (Bartlett 1936; Routledge & Swartz 1991); (iii) the augmented Poisson, or negative binomial function, $\sigma^2 = \mu + a\mu^2$ (Hanski 1982; Routledge & Swartz 1991; Perry & Woiwod 1992); (iv) the extended power function, $\sigma^2 = \mu + a\mu^b$ (Perry & Woiwod 1992); and (v) the split domain power plot (Perry & Woiwod 1992).

There has been some debate over which model is most appropriate when low mean densities are included (Routledge & Swartz 1991, 1992; Perry & Woiwod 1992; Lepš 1993). The over-dispersed Poisson sampling model and its related statistics described earlier may shed some light on this controversy. If the data are in the form of unreplicated counts measured repeatedly through time, then an assumption of Poisson sampling error may not be unreasonable. When the expected density is low then most of the variation between values of N_t will be due to Poisson error, not variation between the values of λ_t. For example, if N_t is negative binomially distributed then the log–log plot has the typical curved shape with the final linear part having a slope of 2. This is because the gamma distribution of λ_t has the relationship $\sigma^2_\lambda = \mu^2_\lambda$, so when the mean density is less than 1 the variance of λ_t decreases rapidly with the mean allowing the Poisson sampling error to dominate. However, as the mean density increases the variance among λ_t increases rapidly, while, as $\sigma^2_{N|\lambda} = \lambda_t$, the Poisson error becomes a relatively insignificant contribution. For example, when N_t is negative binomially distributed the relationship between the variance of the counts and the mean is of the form:

$$\sigma^2_N = \mu + a\mu^2.$$

The parameter a is $1/k$, the shape parameter of the distribution. It is also the $\mathrm{CV}^2(\lambda_t)$. This form of variance–mean relationship could easily appear even if the underlying distribution was not a negative binomial, in which case the $\mathrm{CV}^2(\lambda_t)$ interpretation

could still be sensible. One feature of this form of relationship is that if we re-organize the formula we get:

$$\frac{\sigma^2 - \mu}{\mu^2} = \alpha.$$

The variability of the density, $\mathrm{CV}(\lambda_t)$, is constant with respect to mean density. Lepš' (1993) observation that at small densities $\mathrm{CV}(N)$ is negatively correlated with the mean is a reflection of the sampling error that dominates at those densities. With a Poisson distribution $\mathrm{CV}(N)$ declines with the mean. His argument that this is an artefact is therefore not strictly true. $\mathrm{CV}(N)$ is measuring, appropriately, the variability of the counts, however it is not measuring the variability of the densities of which those counts are estimates.

This relationship ($\sigma^2 = \mu + \alpha\mu^2$) is common to many long-tailed distributions, e.g. Polya-Aeppli, Neyman Type A (Freeman 1980).

The literature on variance–mean relationships has many examples where the linear portion has a slope different from 2; implying that the underlying dynamics are functions of mean density. A sensible generalization of the model $\sigma^2 = \mu + \alpha\mu^2$ is the extended power or Nelder model (Perry & Woiwod 1992):

$$\sigma^2 = \mu + \alpha\mu^\beta$$

This model was compared with alternatives by Perry & Woiwod (1992) and found to be one of the two best-fitting models in a variety of data sets (the other was a split line regression), with little to choose between them. Our approach provides an *a priori* rationale for using this variance–mean formula for count data rather than the more *ad hoc* polynomial or split line regressions.

If the extended power or Nelder model is appropriate, then when we reorganize the formula we find that

$$\frac{\sigma^2 - \mu}{\mu^2} = \alpha\mu^{\beta-2}.$$

$\mathrm{CV}(\lambda_t)$ will now be linear when plotted against mean density on a log–log plot.

We suggest that while fitting the model may best be done using log (variance) versus log (mean), graphs of variability (or log (variability)) against the mean (or log (mean)) are much easier to interpret. Unfortunately, because the sample estimates of $\mathrm{CV}^2(\lambda)$ can go negative (implying the population value is close to zero), the parameters α and β are best estimated by a nonlinear regression fit of the above equation or the Nelder model.

(*d*) *Making comparisons between species*

Most of the interest in measuring and describing population variability has centred on between-species comparisons. Here, for simplicity, we consider the problem of comparing variability in just two species. As already noted, for many species population variability and mean population size are correlated and attempts to make general statements about variability may often (but not always) be compromized by this correlation. However, it is possible to make general statements on the comparative variability of two species using variability–mean plots, provided sampling has been at suitable spatial and temporal scales. Two separate situations must be considered.

(i) *The data for the two species come from separate studies*

Here, there are two distinct circumstances:

1. If the variabilities of both species are constant with respect to the mean ($\beta = 2$ in the Nelder model), then the variability of species A can simply be compared to that of species B. It is then possible to make simple statements about which species is more variable. However, given the unreliability of sample estimates of variability, confidence intervals or an appropriate significance test should be presented. If the statistical distributions are very long-tailed, the test and associated confidence intervals could be over optimistic. Furthermore, if the degree of skewness in the distributions differs between the two species, and/or the sample sizes are different, then the variabilities if based on CV may differ only because of varying levels of sample bias (McArdle *et al.* 1990).

2. If the variabilities of one or both of the species is not constant with respect to the mean then any conclusions are limited strictly to the range of means studied. For example, in figure 4*a* it is possible to say that species A is more variable than species B over the range of densities measured. However, if the ranges of the variabilities overlap then no general statement is possible. This is because it is possible to have a situation like that of figure 4*b* where A and B are negatively correlated and A is always more variable than B, e.g. sites s_1 and s_2. It is also possible to have a similar situation when the species densities are positively correlated, e.g. figure 4*c*. Because the two species were recorded in separate studies, the way the species would vary together is unknown. Of course, in any specific situation the values of CV or SD[log (N)] for the two species can be compared, provided the mean densities are known, but no general statements can be made.

(ii) *The data for the two species come from the same study*

Although it is possible to compare variability–mean plots, this does not use the information on the intercorrelation of the densities of the two species. A better way of measuring relative variability that reflects what is observed more directly may be to calculate the proportion of sites (or occasions for temporal sampling, temporal plotting) on which species A was more variable than species B. As the comparisons are being made on data taken at the same time, in the same place, they have biological meaning. If multi-species comparisons are planned then these proportions could be put in a species by species comparison matrix and analysed using a multi-dimensional scaling technique (Digby & Kempton 1987). This would reflect the complexity implicit in such a comparison; it is possible that there may be a simple

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

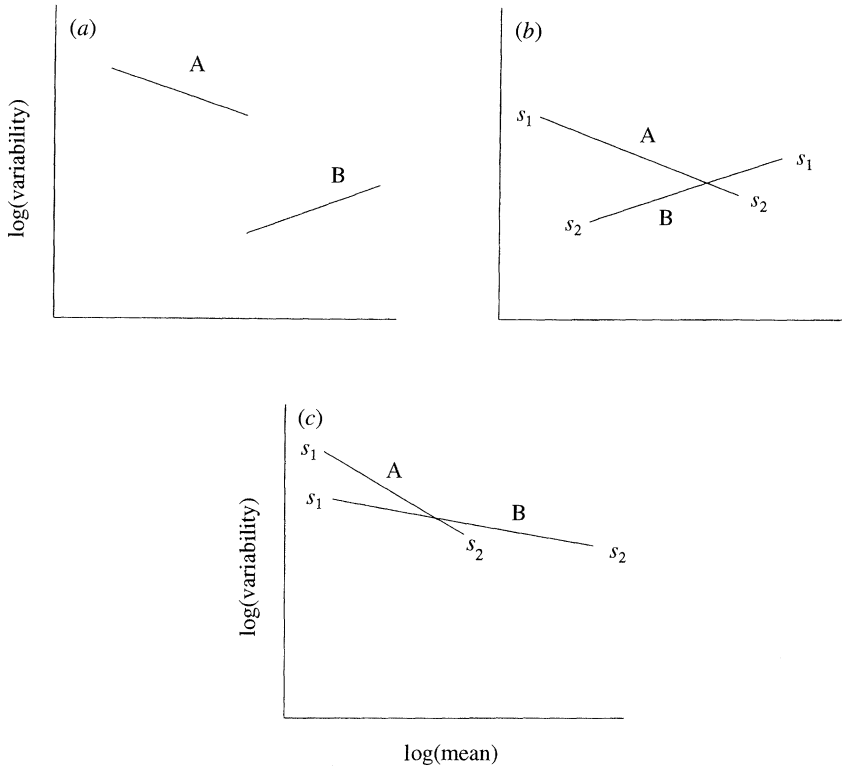

Figure 4. Comparing variabilities between species. (*a*) Species A and B can be compared directly: A is always more variable than B. (*b*,*c*) The species cannot be compared directly if the species abundances are correlated. If they are negatively correlated (*b*), A could always be more variable at site s_1 and site s_2, A is more variable than B. The same can occur if the species are positively correlated as in (*c*).

uni-dimensional ranking such as some workers have tried to impose, but in general it is most unlikely.

(*e*) *Inter- and trans-specific variability–mean plots*

Whilst inter- and trans-specific variance–mean relationships exist, it does not follow that they provide a basis for removing the effect of the intra-specific mean on individual variability values. In figure 5 we present a hypothetical set of variabilities (say values of SD[log (N)] or CV(N)], one value per species. They appear to be independent of the mean. However, when we superimpose the intra-specific variability–mean relationships it is clear that they are not. Any attempt to relate variability to other factors (e.g. environmental ones) will inevitably confound the effect of the factor on the mean.

Various methods which have been used in an attempt to account for differences in mean abundances are likely to fall foul of this same problem. These include multiple regression (e.g. Pollard & Yates 1992; Schoener & Spiller 1992), and the omission of values with low means (e.g. Wolda 1983*a*; Roubik & Ackerman 1987; Wolda *et al.* 1992; Lepš 1993). These try to remove the effects of the inter-specific variability–mean relationship while leaving in place some of the effects of the intra-specific one.

Some studies use the mean or median of several variability values for a species to provide a single value that can then be compared between species (e.g. Rice *et al.* 1983; Ostfeld 1988; Pimm *et al.* 1988; Sutherland & Baillie 1993). If the variability values represent a random sample of variabilities from over the entire range of that species – so that the average value can be taken to represent the typical value for the species – then it may be possible to compare it with one from another species. The statement is then possible 'species A is typically more variable than species B'. Problems arise when the worker wishes to investigate the relationship between these variabilities and some third factor. As the variabilities may be related to the mean abundances within a species, any observed relationship between the factor and variability may be the result of the relationship between the factor and the mean, as in figure 6. Only by partialling out the mean using the *within-species* variability–mean relationship can the comparison validly be made.

(*f*) *Variance component estimation by analysis of variance*

Clearly it will often be desirable to separate the sampling error from the estimate of the variability of the underlying densities. If the counts (N_{t_i}) have been replicated ($i = 1, \ldots, n$) at each time period, then the sampling error at each period t can be estimated (B. H. McArdle & K. J. Gaston, unpublished results). It is then in principle possible to use Analysis of Variance techniques of variance component estimation to estimate the between-density variance. If the log (N_{t_i}) values are available (i.e. there are no zeros in the time

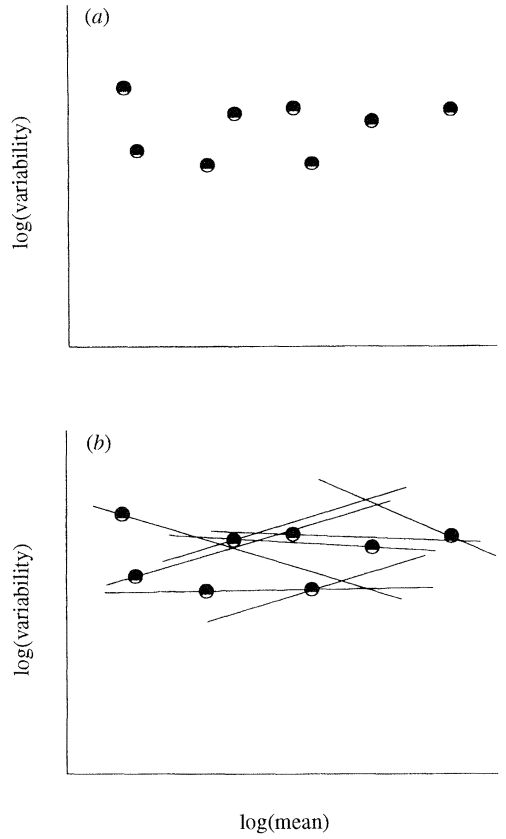

Figure 5. Inter-specific variability–mean plot. Eight species where (*a*) there appears to be no relationship between variability and the mean, but (*b*) when the intra-specific relationships are superimposed, the complexity of the situation becomes apparent.

series) then this process is straightforward (e.g. Sokal & Rohlf 1981). If any of the values of N_{t_i} are zeros then the logarithmic scale is impractical and the analysis must be performed on the untransformed data. The estimated between-density variance component can then be converted to a CV. There may be problems with the analysis of untransformed data since the assumption of homogeneity of error variance is bound to be violated. However, recent work suggests that some of the variance estimation algorithms are robust to this assumption (Kleffe *et al.* 1991).

If a nested or hierarchical sampling design has been employed these variability estimates could be used to define the variability–mean relationship for any given level of the design. There is no reason to assume that the variability–mean relationship is the same at every level of the design. Attempts to do simple nested analysis of variance on hierarchical designs for spatial variability have typically ignored the variability–mean relationship, assuming that a logarithmic transformation will remove it (i.e. $\beta = 2$ in the Nelder model), and have often used the $\log(N+1)$ transformation which will distort the picture still further. It is probably more informative to actually characterize the variability–mean relationship at each level of the design, by doing a series of one-way analyses, so as to allow more reliable comparisons to be made.

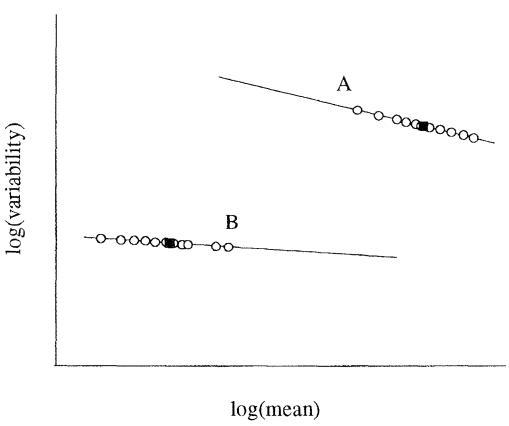

Figure 6. Differences between average variabilities. It is possible to assert that species A is more variable on average than species B, but it is only possible to correct for the difference between the mean abundances by using the within-species relationship.

(*g*) *Variance component estimation in log–linear models*

Recent developments in the theory of log–linear models have raised the possibility of estimating SD[log (λ_t)] directly even if there are sampling zeros present. Log–linear models are a family of linear models that can fit:

$$\log(\lambda_t) = \mu + \alpha_t,$$

where the observed values N_{t_i} are from a Poisson distribution with expected value π_t. The theory of generalized linear mixed models (GLMMs; Schall 1991; Breslow & Clayton 1993) or generalized estimating equations (GEEs) as described by Waclawiw & Liang (1993) allow variance component estimation in the context of log–linear models. There is therefore the prospect of estimating SD[log (λ)] directly. This work is currently in progress.

(*h*) *Detecting patterns within time series*

We have been discussing measuring variance or variability over entire time series and looking for patterns between such series (e.g. variance–mean plots). However, some authors have looked for patterns within time series. In the past most work has been done to detect or describe periodicity (e.g. Moran 1953; Bulmer 1974; Campbell & Walker 1977; and Tong 1977 on the Canadian lynx data alone). Most studies have used either periodograms (e.g. McArdle & Blackwell 1989) or spectral analysis (e.g. Henttonen *et al.* 1985). These techniques are essentially identical, depending in essence on a decomposition of the total variance of the time series into components attributable to cycles of varying wavelength (see Diggle (1990) for a description of the techniques).

Lepš (1993) has suggested that the pattern analysis

techniques commonly used in spatial analysis (e.g. Greig-Smith 1964; Hill 1973; Mead 1974; Usher 1975) can be used to investigate patterns within time series. These techniques re-express the variance into comparisons made at different scales within the series. In this way they can detect periodicities in the data. We note these techniques here only because they are analyses of temporal variance, a detailed discussion lies beyond the scope of this paper.

7. PATTERNS IN THE TEMPORAL VARIABILITY OF ABUNDANCES

A number of patterns in the magnitude of the temporal variability of abundances (over and above those discussed in the context of its measurement; e.g. scale, length of time series) have been postulated, either on theoretical or on empirical grounds. In this section we review some of these patterns. Because of the methods employed, serious question marks must be raised over the results of most, if not all, empirical studies of such patterns which have been performed to date. The primary faults are: (i) the use of inappropriate measures of abundance; (ii) the use of inappropriate measures of variability; (iii) failure to standardize the lengths of time series; (iv) failure to appropriately account for the dependence of variability measures on the mean (the necessary data are seldom available); and (v) failure to consider the effects of spatial scale (McArdle *et al.* 1990; McArdle & Gaston 1992; Xia & Boonstra 1992). Indeed, Xia & Boonstra (1992) remark, solely with regard to (i), that '... most estimates of temporal variability of population density reported for different species or for the same species in different geographical areas are not directly comparable...'. We shall therefore emphasize theoretically predicted patterns and shall not dwell on the results of studies which have, explicitly or otherwise, attempted to test them. Nonetheless, at the start of the section concerned with interactions between a given factor and the temporal variability of abundances, references both to associated theoretical and empirical work (whether significant relationships were found or not) are provided.

Our discussion of patterns is based on the scenario in which for each site:time combination an unreplicated count or estimate of density is available, and in which zeros are retained. That is, we are dealing with the temporal variability of numbers at a site. This is the situation which pertains to the Rothamsted aphid and moth data sets (Taylor 1986), which have proven so important in developing ideas about fluctuations in animal abundances (e.g. Taylor & Woiwod 1980; Hanski 1982; McArdle *et al.* 1990). It is also the circumstance for which data are perhaps easiest to obtain.

The possible relations are considered between various factors and: (i) the magnitude of variabilities at a given mean abundance; and (ii) the magnitude of the slope relating variability and the mean abundance (positive if variability increases with the mean, negative if it decreases, and zero if it is constant; note that the variance about such relationships is usually sufficiently small that distinguishing between constancy and the absence of relationship is not a problem), assuming that slopes are compared over a similar spread of means. Patterns with individual factors are discussed on the assumption of *ceteris paribus* (all other things being equal). Although this is often, if not usually, false (e.g. Gaston & McArdle 1993), given our present understanding of patterns in the temporal variability of numbers at a site it provides the simple framework that is required.

The factors whose interactions with variability are discussed are divided into three groups. That is, those which are intrinsic to the organism concerned and affect its temporal variability, those which are extrinsic to the organism and affect its temporal variability, and those which are a consequence of the level of temporal variability.

(*a*) *Intrinsic factors*

(i) *Taxon* (Connell & Sousa 1983; Schoener 1985, 1986, 1990; Joern & Pruess 1986; Takeda 1987; Ostfeld 1988; Owen & Gilbert 1989; Hanski 1990; Andrews 1991; Crowley & Johnson 1992; McArdle & Gaston 1992; Xia & Boonstra 1992)

To the extent that closely related species tend to have more similar dynamics in their numbers than distantly related species, there will be a phylogenetic component both to the magnitudes of variabilities for any given mean, and to the slope of the relationship between variability and the mean. This observation finds expression in the long-held belief that there are important differences between the dynamics of the numbers of individuals of arthropod (notably insects) and of vertebrate species, with the former being characterized by wider fluctuations than the latter. Ironically, although possible differences between distantly-related groups of species have attracted perhaps more speculation and analysis than any other pattern in the temporal variabilities of numbers at a site, reliable determinations of such differences seem likely to long remain some of the most difficult to achieve. The obstacle lies in generating truly comparable measures (McArdle *et al.* 1990; Xia and Boonstra 1992). It is particularly difficult to determine variabilities at similar mean abundances and at similar scales for very different groups of animals. Indeed, it is tempting to suggest that many general ideas about differences in the variabilities of different taxa may be misconceptions based on differences in overall abundances and in scale.

Should there indeed be a phylogenetic component to the magnitude of temporal variabilities in numbers at a given mean abundance, or to the slope of the variability–mean relationship, it will generally be necessary to account for the relatedness of taxa (e.g. Harvey & Pagel 1991; Gittleman & Luh 1992) in analysing inter-specific patterns in variabilities.

(ii) *Body size* (Gaston 1988; Gaston & Lawton 1988*a*,*b*;

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Owen & Gilbert 1989; Pimm 1991; Loiselle & Blake 1992; Sutherland & Baillie 1993)

Logically, it seems unlikely that differences in body size have a direct effect on either the magnitude of variabilities at a given mean abundance, or the slope of the variability–mean relationship. Interactions may, however, result from observed correlations between body size and various other variables which may have direct effects on variabilities. Relationships have been documented, for example, between body size and density dependence (Woiwod & Hanski 1992), size of geographic range (Gaston 1990), rate of increase (Fenchel 1974; Peters 1983), feeding specificity (Hansen & Ueckert 1970; Jarman 1974; Wasserman & Mitter 1978; Niemela *et al.* 1981; Gaston & Reavey 1989), mean density (Damuth 1987; Currie 1993), dispersal ability (Rapoport 1982) and susceptibility to environmental perturbation (Wasserman & Mitter 1978; Cawthorne & Marchant 1980; Lindstedt & Boyce 1985). Given that relationships between body size and several of its correlates vary with the taxonomic breadth of comparisons (e.g. within genera, within families, across families; abundance: Nee *et al.* 1991; rate of increase: Williamson 1989), consistent patterns between body size and variability seem unlikely.

Body size can also interact with measured variability via the choice of sample unit size and extent. When studies compare relatively closely related taxa no correction is usually made in the sampling design for differences in body size or related biological scale effects. When comparisons are being made between more distantly related taxa (e.g. birds and insects), implicitly the spatial sampling scale at least has been crudely adjusted.

(iii) *Population growth rate* (Spitzer *et al.* 1984; Spitzer & Lepš 1988; Pimm 1991; Hanski & Woiwod 1993; Sutherland & Baillie 1993)

The outputs of simple single-species single-population models have different relationships between temporal population variability and population growth rates, dependent on how they are constructed (e.g. Hassell *et al.* 1976; Whittaker & Goodman 1979; Pimm 1984*b*, 1991). For example, in some simple deterministic density-dependent models, variability increases with population growth rates, with progressively higher rates leading from stable equilibria through limit cycles to chaos. This broad pattern persists if a stochastic component is incorporated in the carrying capacity, such that it fluctuates through time. Here, populations with higher growth rates will track the carrying capacity more closely and hence fluctuate more widely. Populations with low growth rates will tend to remain stable. A rather different result is obtained if a stochastic element is included in the population growth rate rather than in the carrying capacity. Here, populations with higher growth rates will tend to be less temporally variable, because they can recover from population lows rapidly. Populations with low average growth rates cannot do so.

Clearly although simple population models have heuristic value, relating their observed outputs to patterns in the real world remains problematic. Not least of these problems is that the population growth rate r is expressed in units of days, months or years, so clearly a comparison of r for aphids with that for elephants would be ludicrous. A more logical statistic to compare is the net reproductive rate R_0 ($\log(R_0) = rG$ where G is the generation time), which is measured on a scale of generation times. When growth rates are compared between species, it seems most likely that populations with high growth rates will, at a given mean abundance, show the greater variability in that abundance. However, no general pattern need necessarily be found to exist.

McArdle *et al.* (1990; see below) argue that positive relationships between variability and the mean are characteristic of boom and bust populations (e.g. pests). Such dynamics are often associated with high population growth rates, suggesting the possibility of an interaction between these rates and the slope of the variability–mean relationship.

(iv) *Feeding specificity* (Watt 1964, 1965, 1968; Rejmanek & Spitzer 1982; Redfearn & Pimm 1987, 1988; Gaston & Lawton 1988b; Owen & Gilbert 1989; Hunter 1991; Pimm 1991)

Considerations of patterns in temporal variabilities in numbers with respect to differences in an organism's feeding specificity are severely complicated by the variety of ways in which this latter variable can be defined. It may be viewed as the number of host species eaten by the consumer species or the number of host species eaten by average individuals of the consumer species (the host range of a species is commonly broader than that of an individual of that species), it may be weighted by the relative level of use of each host species (many hosts may contribute little to the intake of an individual or species) or by the taxonomic relatedness of the host species (closely related host species may be weighted less than distantly related). Debate as to the relationship between feeding specificity and the temporal variability of numbers has largely (although not exclusively) concerned simply the numbers of hosts eaten by a consumer species, but conclusions might be substantially altered were these other emphases to prove of major importance.

Arguments have been proffered both in favour of patterns of increasing and of decreasing variability in numbers at a site with reduced host specificity (see Pimm (1991) for discussion). A larger number of hosts may serve to buffer a species against fluctuations in the abundance of any one host, thus generalists may have temporally less variable populations than specialists (MacArthur 1955). Equally, an ability to feed upon a large number of hosts may mean that a species can respond numerically to outbreaks in any one, generalists thus may have more variable numbers than specialists (Watt 1964).

(v) *Cycles and trends* (Hansson & Henttonen 1985*a*,*b*;

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Henttonen *et al.* 1985; Saitoh 1987; Mackin-Rogalska & Nabalgo 1990; Hansson 1991; Pimm 1991; Sandell *et al.* 1991; Pollard & Yates 1992; Wolda 1992; Wolda *et al.* 1992; Xia & Boonstra 1992)

The addition of cycles to an underlying level of stochasticity will lead to an increase in variability at a given mean abundance. The standard deviation of log-transformed densities has commonly been used as an index of cyclicity, larger values being regarded as indicative of cycling (e.g. Hansson & Henttonen 1985*a*,*b*, 1988; Henttonen *et al.* 1985; Mackin-Rogalska & Nabalgo 1990). However, although cycling is likely to increase variability, it does not follow that high variability implies cycling, and for this and a number of other reasons application of this technique seems seriously flawed (Sandell *et al.* 1991; but see Hansson 1991). In addition, there seems to have been little attempt to ensure that comparisons are based on similar means.

The presence of trends in a time-series of abundances will likewise tend to increase measured variabilities, whether the trends are positive or negative. Indeed, for many analyses of variability it may be necessary to detrend data, although this is not always readily achieved. In particular, trends become difficult to detect when means are low and temporal variabilities are dominated by sampling error, an observation of some importance to conservation. Whether data should or should not be detrended will be determined by the objectives of the study. If the aim is to measure the average short term variation in the dynamics of numbers, then detrending would usually be appropriate. This might be the case if, for example, numbers had been declining for some time, and conservation strategies were to be put in place to halt this decline. The expected short term variation might be useful in planning an appropriate strategy.

A tendency for cycling to be associated with high mean abundances, will lead to the slope of the variability–mean relationship becoming positive. Consistent trends will nearly always be correlated with larger means (by definition), so trends will likewise tend to generate positive slopes to variability–mean relationships.

Note that all the above remarks only pertain when a measure of overall variability including trend is being used (see § 2).

(vi) *Overall mean* (Hanski 1982; Karr 1982; Joern & Pruess 1986; Roubik & Ackerman 1987; Gaston 1988; Gaston & Lawton 1988*a*,*b*; Samways 1990; McArdle & Gaston 1992; Hanski & Woiwod 1993; Sutherland & Baillie 1993)

There has been much speculation that rare species have more variable numbers than do common species. If true, this might have potentially important applied implications, especially for conservation (Gaston & McArdle 1993). Analyses have, however, almost invariably been founded on one value of mean and variability per species, with no standardization of means on the basis of intra-specific variability–mean relationships (comparisons of variabilities would need to be based on equivalent local mean abundances, for species which differed in their mean abundances across sites). This prevents any empirically based general statements about species relative variabilities.

The interaction of the slope of the variability–mean relationship with overall mean abundance has received some interest in the context of descriptions of the former based on temporal Taylor power plots. A positive correlation between the slope of the temporal Taylor power plot and mean abundance has been documented (Hanski 1982; Taylor & Woiwod 1982; Taylor 1984, 1986). This relationship is almost certainly an artefact arising from the presence of Poisson sampling error at low densities, which forces the variance–mean relationship to conform to the Poisson 1 : 1 line (Hanski 1982; Taylor & Woiwod 1982). This makes the Taylor's power plot nonlinear and shallow at low densities. Species with low overall means will have their slope dominated by this effect. Species with high overall means will not.

As yet there seems little basis for arguing that mean abundances have any consistent direct effect on either temporal variabilities in numbers or the slope of the variability–mean relationship. They are, however, correlated with other variables which are postulated to interact with variability, directly or indirectly (e.g. body size: Damuth 1987, Currie 1993; range size: Brown 1984; Gaston & Lawton 1990).

(vii) *Density dependence* (Anderson *et al.* 1982; Hanski 1982, 1990; Hanski & Tiainen 1988; Crowley & Johnson 1992; Hanski & Woiwod 1993)

Most effects of density dependence on temporal variabilities can be expected to be on the relationship between variability and the mean, rather than on variabilities for a given mean. However, low variabilities tend to imply that density-dependent processes are operating. The converse inference, that density dependence leads to low variability, is not tenable. If the environment is variable or density dependence is delayed, the temporal variability of populations may be high regardless of the operation of density-dependent processes.

Provided the carrying capacity K is driven by environmental variation in such a way that SD[log (K)] does not have a positive relationship with log (mean K), then the slope of the relationship between variability and the mean (the density dependence of variability *sensu* Hanski (1990)) will be negative if populations are density dependent. Hanski & Tiainen (1988) argue that their demonstration that territorial British bird species had lower slopes of temporal Taylor power plots than did non-territorial species could be explained on the basis that territoriality is a prime example of a density-dependent process.

As yet, there are no published analyses of the frequency with which different values for the slope of the variability–mean relationship occur when those slopes have been estimated using an appropriately nonlinear model. We submit, however, that it would be unwise to regard relationships indicative of density independence (slope = 0) as the norm, given that recent analyses of large numbers of time series using

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

various methods purported to test for density dependence have demonstrated the phenomenon to be common (Hanski 1990; Woiwod & Hanski 1992). Using the Taylor power plot model of the variance–mean relationship, the frequency of negative variability–mean relationships (b of temporal Taylor power plot < 2) was high (Taylor & Woiwod 1980, 1982; Anderson *et al.* 1982; Hanski 1990; McArdle *et al.* 1990), whereas under reanalysis this frequency will decline, it seems probable that many relationships will remain negative.

(viii) *Dispersal/connectivity* (den Boer 1981, 1985, 1990)

The degree of inter-connectedness of local populations, ranging from discrete populations to a continuous surface with areas of relatively high and low density, has potentially profound implications for their temporal variabilities. High inter-connectedness leads to individual populations that are at low levels or have become extinct being 'rescued' by immigration of individuals from other populations, tending to smooth out local population fluctuations (reducing their individual variabilities), and also reducing the variability of the summed populations ('spreading of risk'; den Boer 1968). Therefore for any given mean, high dispersal and connectivity will tend to reduce temporal variability in numbers.

There is no obvious reason why differing levels of connectivity *per se* should impact on the slope of the variability–mean relationship, with one important exception. If connectivity is based on density-dependent dispersal (see § 7*a*(vii)), then slopes will tend to be negative if local populations are inter-connected.

(ix) *Size of geographic range* (Gaston 1988; Gaston & Lawton 1988*a*,*b*; Spitzer & Leps 1988; Glazier 1986; Sutherland & Baillie 1993)

The size of a species geographic range can be measured in two distinct ways: (i) its extent of occurrence: the distance or area between the spatial limits to the localities at which the species has been recorded or is predicted to occur; and (ii) its area of occupancy: the number of sites or the area it actually occupies within the limits to its occurrence (Gaston 1991*a*). The larger the area occupied, the more local populations there are to provide immigrants, the more likely there will be a rescue effect, and thus the greater the likelihood that fluctuations in any one population will be damped. That is, the greater the area of occupancy, the lower temporal variabilities of local numbers are likely to be at a given mean abundance. In principle, greater extents of occurrence may be associated with greater variabilities at a given mean, because local populations could be more distantly separated. This would reduce the likelihood of any rescue effect. Such a pattern seems unlikely however, because extents of occurrence and areas of occupancy tend to be positively related (Gaston 1991*a*).

Contrary to the above, Glazier (1986) suggests two bases for a positive relationship between variability in numbers at a site and range size (by inference, area of occupancy). The first is a selective extinction argument, with a positive relationship resulting from the loss of species with small geographic ranges and high local variability in numbers. The second derives from the claim that widespread species are good colonists which opportunistically exploit temporary or fluctuating habitats or resources.

Whilst we would favour the likelihood of a negative relationship between variability and range size, clearly there are ample grounds for speculation on the topic. Documentation of the actual interaction, if any, would need to address the potentially confounding effect of the commonly observed relationship between range size and local abundance (e.g. Brown 1984; Gaston & Lawton 1990).

(*b*) *Extrinsic factors*

(i) *Habitat/environmental temporal variability* (Brewer 1963; Wolda 1978, 1983*a*,*b*; Ohgushi & Sawada 1981; Wolda & Galindo 1981; Tiainen 1983; Wolda & Roubik 1986; Roubik 1989; Rejmanek & Spitzer 1982; Van Dijk 1986; Roubik & Ackerman 1987; Pimm & Redfearn 1988; Spitzer & Lepš 1988; Virkkala 1989; Ebeling *et al.* 1990; Pimm 1991; Loiselle & Blake 1992; Wolda *et al.* 1992).

The densities of animals in different habitats can have different variabilities. The different variabilities are generally thought to be driven by the levels of temporal variability exhibited by the habitats. The more variable the environment, the greater the temporal variability in numbers is likely to be for a given mean abundance. Similar conclusions pertain whether background levels of environmental variability are considered or the frequency and severity of catastrophes (infrequent but severe environmental perturbations, whose impact is, at best, only weakly a function of levels of abundance). However, the strength of the interaction between temporal variabilities in environmental factors and in numbers at a site will depend on the form of the environmental variation, and the rapidity with which a population responds to it.

A number of factors may serve to complicate such a scenario. In particular, the suggestion that disturbed (and hence temporally variable) habitats tend to be occupied by species with high rates of population growth, and less disturbed habitats by species with low rates of population growth. It has already been suggested that population growth rates and levels of temporal variability in numbers may be associated.

The tendency for the temporal variability of abundances to increase with the length of a time series has been mentioned earlier (see § 5), along with the argument that this is a result of temporal environmental variabilities, which also tend to increase with time ('red-shift').

The interaction between different patterns of temporal variability in the environmental conditions at sites, and the slopes of temporal variability–mean abundance relationships were identified by McArdle *et al.* (1990):

1. If slopes are zero, then the variability of the populations measured over time is roughly constant

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

from site to site. If density dependence is a major determining factor then such slopes imply that K is highly variable and that there is no relationship between SD[log (K)] and log (mean K).

2. If slopes are positive, then temporal variability is greater at good sites, i.e. good sites are subject to times of boom and bust. This is the pattern one might expect to see in a pest species prone to outbreaks. If density dependence is a major determining factor then such slopes imply that there is a positive relationship between SD[log (K)] and log (mean K).

3. If slopes are negative, then temporal variability tends to be less at good sites than bad ones, i.e. marginal habitats go up and down more than good ones. If density dependence is a major determining factor then such slopes imply that there is a negative relationship between SD[log (K)] and log (mean K).

It has often been stated that populations at the edge of a species' geographic range are more susceptible to density independent factors than those at the centre (Huffaker & Messenger 1964; Richards & Southwood 1968; Coulson & Whittaker 1978). It might be thought that temporal variabilities will thus follow suit. Such an argument is potentially seriously confounded by differences in abundance towards the edge of the range (Hengeveld & Haeck 1982; Brown 1984), and by any broad geographical gradients in the variability of populations.

Migratory behaviour can be considered as one strategy to reduce the effects of seasonal temporal environmental variability, and to exploit spatial environmental variability. Indeed, interactions between migratory tendencies and levels of temporal variability have been commented upon or explored in several studies (Rejmanek & Spitzer 1982; Pollard 1984; Ebeling *et al.* 1990; Pimm 1991). The variety of forms of migratory behaviour and reasons for it suggest that there is unlikely to be any general relationship between the expression of the behaviour and temporal population variability at a given mean.

(ii) *Richness of predators* (Pimm 1991; Redfearn & Pimm 1992).

The richness of predators attacking a host can be hypothesized to interact with its temporal variability in numbers at a given mean in three different ways (Redfearn & Pimm 1992). First, a greater number of predatory species may impose higher mean mortality rates and thus reduce a host's population growth rates (and hence population variability) more than a small number of predators. Second, a greater number of predatory species may provide more reliable control of a host species population. There is a greater likelihood that there will always be at least one predator that is sufficiently abundant to prevent host numbers escaping to high levels with the result that host population variability will be kept low. Third, the level of host population variability may itself limit the number of predator species which can successfully attack it. Hosts with highly variable populations may support few species of predators.

Yet more predatory species may tend to feed upon a host when it is at high densities. This may lead to a tendency for hosts exploited on average by a relatively large number of predators to have a greater likelihood of negative variability–mean relationships (i.e. density-dependent mortality).

(iii) *Latitude* (Hansson & Henttonen 1985*a*; Mackin-Rogalska & Nabalgo 1990; Xia & Boonstra 1992; Pollard & Yates 1993).

Obviously latitude *per se* can have no direct effect on temporal variabilities in numbers. However, once again, it is correlated with a variety of other variables which may have direct effects on variabilities or are themselves correlates of variables which may have direct effects. These include environmental variability (Stevens 1989), taxon (few taxa occur at all latitudes or are equally speciose at those at which they do occur; Pianka 1966; Brown 1988; Gaston 1991*b*), mean abundance (Currie & Fritz 1993), and geographic range size (Stevens 1989). Indeed, several of the studies cited under 'Habitat/environmental temporal stability' contrast variabilities in temperate and tropical habitats, and might thus equally be regarded as exploring latitudinal patterns.

(*c*) *Consequences:*

(i) *Risk of extinction* (Karr 1982; Wright & Hubbell 1983; Diamond 1984; den Boer 1985; Pimm *et al.* 1988; Schoener 1991; Pollard & Yates 1992; Schoener & Spiller 1992; Tracy & George 1992; Pimm 1993)

Unsurprisingly, two methodological considerations gain particular significance in considering the association between local population variabilities and risks of extinction. These are namely the distinctions between sampling and structural zeros, and between variabilities based on measures of density and on measures of population size (Gaston & McArdle 1993). Failure to determine correctly in a time series which zeros are sampling and which are structural not only affects calculations of temporal variability (see §4), but also calculations of extinction rates (in this context sampling zeros are termed pseudo-extinctions) and of turnover (sampling zeros generate pseudo-turnover; Lynch & Johnson 1974; Nilsson & Nilsson 1983, 1985). The distinction between variabilities based on densities and on population sizes is important, because arguments as to the effect of differences in variabilities on the likelihood of extinction are based, although not always explicitly, on variabilities in population sizes.

It is widely understood that, at a given mean abundance, populations which fluctuate in size to a larger extent will have a greater probability of extinction (Leigh 1981; Diamond 1984; Pimm *et al.* 1988). They will attain low population sizes more frequently, and thus in any one time period the likelihood that all individuals will by chance suffer mortality is greater. A similar argument cannot be made with respect to the variability in population densities, because these are unlikely to represent a constant proportion of the size of a population. Even were they to do so over much of the range of values of

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

population size, they cannot do so when population sizes are small. However, it need not necessarily follow that there will be no relationship between variability in population densities and extinction rate.

Let us assume for a moment that local numbers do represent a constant proportion of overall populations, or that variabilities are based on population sizes. Then, it seems likely that populations can only persist at very high variabilities if they have high means, and that as a result the minimum abundance value observed to be associated with a given level of variability will steadily increase with that variability. Simple predictions of the interaction between the slope of the variability–mean relationship and risk of extinction are difficult to realize. They depend essentially on the relative influences of variabilities and means on this risk.

8. CONCLUSIONS

The description of the essential dynamics of a time series of abundances using a measure of variability is an attractive proposition. It holds out the possibility of making simple intra- and inter-specific comparisons of the patterns in and determinants of those dynamics. The attraction is, however, a potentially beguiling one. Although measures can be derived that capture the quantity which ecologists recognize as variability, a large number of considerations must be taken into account before any sensible inter-specific comparisons can be achieved. An understanding of what these factors are is growing apace, methods of accommodating them in most cases need development. We remain hopeful that these can yet be achieved.

K.J.G. is grateful to the Royal Society for providing support for a study visit to the School of Biological Sciences, University of Auckland, and to the staff of the school for their hospitality.

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Received 15 September 1993; accepted 23 March 1994

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES