Density Dependence, Regulation and Variability in Animal Populations

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Phil. Trans. R. Soc. Lond. B 1990 **330**, 141-150
doi: 10.1098/rstb.1990.0188

Density dependence, regulation and variability in animal populations

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SUMMARY

This paper reviews a series of approaches to the study of density dependence, regulation and variability in terrestrial animals, by using single-species, multispecies and life table time series data. Special emphasis is given to the degree of density dependence in the level of variability, which is seldom discussed in this context, but which is conceptually related to population regulation. Broad patterns in density dependence, regulation and variability in vertebrates and arthropods are described, with some more specific results for moths and aphids. Vertebrates have generally less variable populations than arthropods, which is the only well documented, consistent pattern in population variability. The degree of density dependence of variability is negatively correlated with the average level of variability, suggesting that generally the more regulated populations are less variable. Most population studies, especially on insects, have involved outbreak species with complex dynamics, which may explain the common failures to detect density dependence in natural populations. In British moths, density dependence is less obvious in the more abundant species. The study of uncommon and rare species remains a major challenge for population ecology.

1. INTRODUCTION

Density dependence, population regulation and variability in population size are three related and recurrently debated concepts in population ecology. Low variability implies the operation of some regulatory processes, which by definition involve one or more density dependent components. But the reverse is not true: not all density dependent processes regulate a population towards a stable equilibrium point or reduce variability.

The purpose of this paper is to present a selective review of studies of density dependence, regulation and variability in terrestrial animals, supplemented with original analyses on moths and aphids. By density dependence I mean 'some dependence of average growth rate on present and/or past population densities' (Murdoch & Walde 1989). Variability refers to the level of variation in population size or density from one generation to another. Population regulation has been given different definitions even in the most recent literature. To some ecologists, regulation is 'the process whereby a population returns to its equilibrium' (Varley *et al.* 1973; Dempster 1983; Sinclair 1989). If such a definition is adopted, it would be preferable to include stable non-point attractors among the equilibria. To many others, however, regulation simply means 'long-term persistence and fluctuations within limits, with the lower limit > 0' (see, for example, Mountford (1988); Murdoch & Walde (1989)), a definition that essentially equates regulation with persistence. In this paper, I will discuss and employ a concept which in a sense unites these two facets of regulation.

This paper is limited to observational data, and no experimental studies or techniques are cited, even if they are often superior to observational studies in answering questions about density dependence and population regulation (Murdoch 1970; Murdoch & Walde 1989; Gaston & Lawton 1987). Table 1 outlines the kinds of data and the types of analyses that have been used to study density dependence and variability in terrestrial animals. The following three sections focus in turn on single-species, multi-species and life table time series data. Most studies are concerned with what happens in local populations, but it is possible that a metapopulation perspective would provide a better understanding of population regulation in some species (§5).

Much of the debate about population dynamics is framed in sharp dichotomies: is there density dependence or not? Are local populations regulated or not? Posing such dichotomies is likely to be misleading, because the answers depend on the spatial and temporal scales under consideration, and on the kind of data available. This paper has been written in the spirit that observational data are better suited for comparative analyses of many species rather than for population dynamic studies of single species.

2. SINGLE-SPECIES TIME SERIES

(*a*) *Conceptual and methodological issues*

The most commonly used measure of variability is

Table 1. *Types of data and analyses that have been used to examine density dependence, regulation and variability in terrestrial animals*

type of data and analysis	object of analysis
single-species time series	
autoregressive and other statistical techniques	density dependence of population change
standard deviation of log-transformed census data	level of variability, population regulation
slope of the temporal variance-mean regression	density dependence of variability (= population regulation?)
multi-species time series	
regression techniques	causal explanation of population regulation
constancy in species composition	mechanisms of population regulation
life table time series	
k factor analysis	density dependence of particular mechanisms

the standard deviation of the logarithms of population sizes, *s*, measured over generations. Unfortunately, there are two major difficulties in using *s* or any other single parameter as a measure of variability of natural populations. First, although *s* is often assumed to be a density independent measure of variability, and hence suitable for comparisons of species varying in average abundance (Connell & Sousa 1983), generally it is not (below). A particular problem is created by time series for rare species with many zeros, in which variability is necessarily underestimated (now using the standard deviation of log $[N+1]$). Second, the value of *s* depends on the spatial and temporal scales of sampling, which greatly complicates most analyses. In the real world, different processes affecting variability operate at different timescales, and there is no guarantee that variability will reach an asymptotic value with time before the population goes extinct (Pimm & Redfearn 1988). Figure 1 gives an example, for five species of forest insects, in which variability continues to increase after 100 years of data-collecting! In brief, simple as the concept of variability is in theory, complex are the problems in using it in practice.

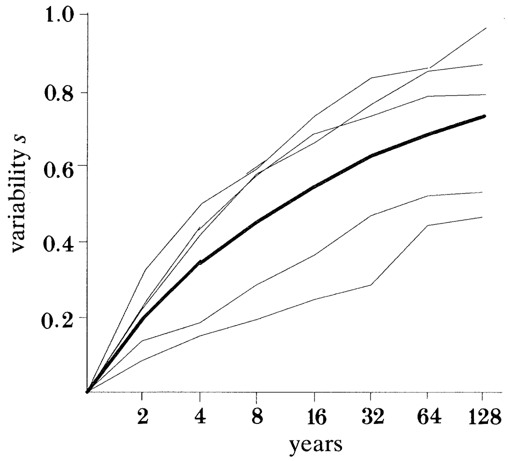


Figure 1. Increase in variability (*s*) in five species of forest insects with increasing length of the census period (the species are *Bupalus piniarius*, *Panolis flammea*, *Lymantria monacha*, *Dendrolimus pini* and *Diprion pini*; thin lines are the averages for four localities, the thick line is the average for the five species; data measure the extent of local and regional population outbreaks, from Klimetzek (1979)). Calculations were done on nested data as explained by Pimm & Redfearn (1988). Analysis of covariance indicated that species, locality and census period all had a highly significant ($p < 0.0001$) effect on *s*.

There has been much debate in the literature in recent years about how to use time series data to show density dependence. Various statistical techniques have been described, discussed and 'tested' by many authors (Morris 1959; Williamson 1972; Bulmer 1975*a*; Slade 1977; Vickery & Nudds 1984; Gaston & Lawton 1987; Pollard *et al.* 1987; Turchin 1990). None the less, many difficulties remain: (i) most techniques are suitable for detecting only linear density dependence, whereas various nonlinearities are common in nature; (ii) most techniques are unsuitable for detecting delayed density dependence, and may underestimate the overall level of density dependence (Turchin 1990); (iii) our chances of detecting density dependence increase with the length of the time series (Hassell *et al.* 1989), hence many failures to detect density dependence may simply be because of short runs of data, and (iv) density dependence may occur only infrequently, and only at some spatial scales. In view of these difficulties, I suggest that observational data are better suited for comparative studies of density dependence rather than for the elusive search of whether density dependence 'exists' or not. Three useful undertakings are to ascertain at which spatial and temporal scales density dependence is strongest (§5), which are the agents of density dependence (the focus of life table studies; §4), and how patterns of density dependence vary between taxa (Fowler 1981) and environments (Stubbs 1977).

Turning to population regulation, the most convincing demonstrations of regulation are expected to come from experimental studies (Murdoch 1970; Sinclair 1989), regardless of which definition of regulation is used (§1). When only observational data are available, one may attempt to show either that the underlying (deterministic) dynamics involve stabilizing density dependence (Taylor & Turchin, in preparation), or that population variability approaches an asymptotic value with time (Murdoch & Walde 1989; regulation used in the sense of persistence). Two problems with the latter approach are that, in fact, variability often increases with time without reaching an asymptotic value (figure 1), and variability often depends on density.

The degree to which the level of variability is density dependent is an interesting question which has not been discussed much in this context. Strongly density dependent variability (s, measured on a logarithmic scale) means that the amplitude of population fluctuations (on an arithmetic scale) is relatively independent of average density, which changes when, for example, different limiting (but density independent) factors become more or less important. Density dependence of variability combines, in a sense, the two notions about population regulation, namely stabilizing density dependence (of population change) and constrained variability. The degree of density dependence of variability is conveniently measured by the slope of the temporal variance-mean regression (Taylor 1961). Note that variability (s) is density independent only if the slope of the variance-mean regression equals two (Hanski 1982).

(*b*) *Patterns of density dependence, variability and population regulation*

(i) *Density dependence of population change*

Several recent analyses of published population studies have concluded that the frequency of significant density dependence in animal populations is surprisingly low, often less than 50% (Dempster 1983; Strong *et al.* 1984; Stiling 1987, 1988; Gaston & Lawton 1987). In the previous section I enumerated several technical reasons for the many failures to detect density dependence. One biological reason, to be further discussed in §2*d*, is the high frequency of outbreak (pest) species among the species that have been studied.

In insects, the type of density dependence has been found to vary with the degree of temporariness of the habitat, from over-compensating density dependence in species living in more-temporary habitats to less severe density dependence in species living in more-permanent habitats (Stubbs 1977). Fowler (1981) suggested that while in large mammals most density dependent change occurs at high densities, in insects most density dependent change occurs at densities far below the environmental carrying capacity (not consistent with Stubbs' findings for species living in temporary habitats). Sinclair (1989) reviews in some detail between-taxon differences in the pattern of density dependence. It would be satisfying to conclude something general about the strength of density dependence in vertebrates versus arthropods, but we have too little comparable data to draw such conclusions.

(ii) *Variability*

A series of recent reviews has examined the level of variability in animal populations. A pioneering study by Connell & Sousa (1983) found no difference between terrestrial vertebrates and arthropods, but their database was limited and taxonomically biased. In the pooled results of many studies, terrestrial vertebrates have significantly less variable populations, on average, than arthropods (figure 2). Previous studies have reported that lizards have especially constant populations among vertebrates (Schoener 1985); that birds have more constant populations than mammals (Connell & Sousa 1983); and that aphids have more variable populations than hoverflies and moths (Owen & Gilbert 1989; figure 3). Some of these conclusions are probably correct, e.g. temperate small mammals tend to have more variable populations than temperate birds (figure 5), but others are based on small and possibly biased samples, and most results are hampered by the technical problems discussed in §2(*a*).

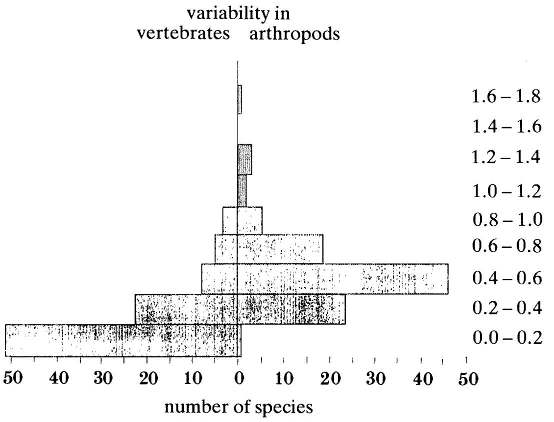


Figure 2. Population variability (s) in 91 species of terrestrial vertebrates (mammals, birds and lizards, from Connell & Sousa (1983); Schoener (1985); Ostfeld (1988); T. Solonen, unpublished data), and in 99 species of terrestrial arthropods (moths, aphids, hoverflies, grasshoppers, etc., from Connell & Sousa (1983); Owen & Gilbert (1989); Joern & Pruess (1986); I. Woiwod, unpublished data). Variability has been measured for generations where possible (most studies). The distributions for vertebrates and arthropods are highly significantly different (two-tailed Kolmogorov–Smirnov statistic 0.58, $p < 0.0001$). Note that average variability in the five forest insects in figure 1 remains between 0.4 and 0.6, the modal class for arthropods in this figure, for the time periods between 5 and 30 years, which bracket the typical lengths of time series data available for most species. The results in figures 1 and 2 are thus consistent with each other.

Theoretical arguments can be developed for both negative and positive correlations between variability and population growth rate (Pimm 1984), and between variability and the degree of polyphagy in herbivorous insects (Redfearn & Pimm 1988); and both negative and positive correlations have been found in empirical studies (table 2). One unexpected pattern to emerge is lack of correlation between variability and latitude in insects (Wolda 1983). Once again, however, it is not clear which of these studies are not compounding variability and density, and which results are not artefacts of the scale of sampling. I conclude that there are no well documented, consistent patterns in variability apart from the difference between vertebrates and arthropods (figure 2).

The broad difference between vertebrates and arthropods should not distract us from the fact that variability is primarily a property of populations living under particular environmental conditions. Recent demonstrations of conspicuously increasing variability in small mammals with latitude in northern Europe (Hansson & Henttonen 1985, 1988) is a case in point. Increasing variability is associated with increasingly regular multiannual cyclicity, with the cycle length

Table 2. *Ecological correlates of population variability in insects*

ecological factor	effect on variability	reference[a]
population growth rate	positive	1
	negative	8
body size	negative	2, 4
polyphagy	positive	2, 6, 5
	negative	7
geographical distribution	positive	2, 3, 4
number of competitors	positive	5
latitude	no correlation	9
	positive	10

[a] 1, Spitzer & Leps (1988); 2, Gaston (1988); 3, Glazier (1986); 4, Gaston & Lawton (1988); 5, Watt (1965); 6, Rejmanek & Spitzer (1982); 7, Redfearn & Pimm (1988); 8, Pimm (1984); 9, Wolda (1983); 10, Hansson & Henttonen (1985).

increasing from 3 years in southern Fennoscandia to 5 years in northern Lapland (Hanski *et al.* 1991). In this case large variability is not associated with lack of population regulation, but to a change from predominantly direct (not delayed) density dependence in the south to delayed density dependence in the north, possibly because of latitudinal shift in the type of predation (Hanski *et al.* 1991).

(iii) *Density dependence of variability*

Figure 3 summarizes the temporal variance–mean regression slopes for aphids, moths and birds sampled throughout the United Kingdom (Taylor & Woiwod 1980, 1982). There are highly significant differences between these taxa, birds having by far the smallest slopes, suggesting that bird populations are more strongly regulated than insect populations. Among birds, territorial species have significantly smaller slopes (average 1.08) than non-territorial species (1.28), which is consistent with the known regulatory function of territoriality (analysis in Hanski & Tiainen (1989)).

(*c*) *Relations between density dependence, regulation and variability*

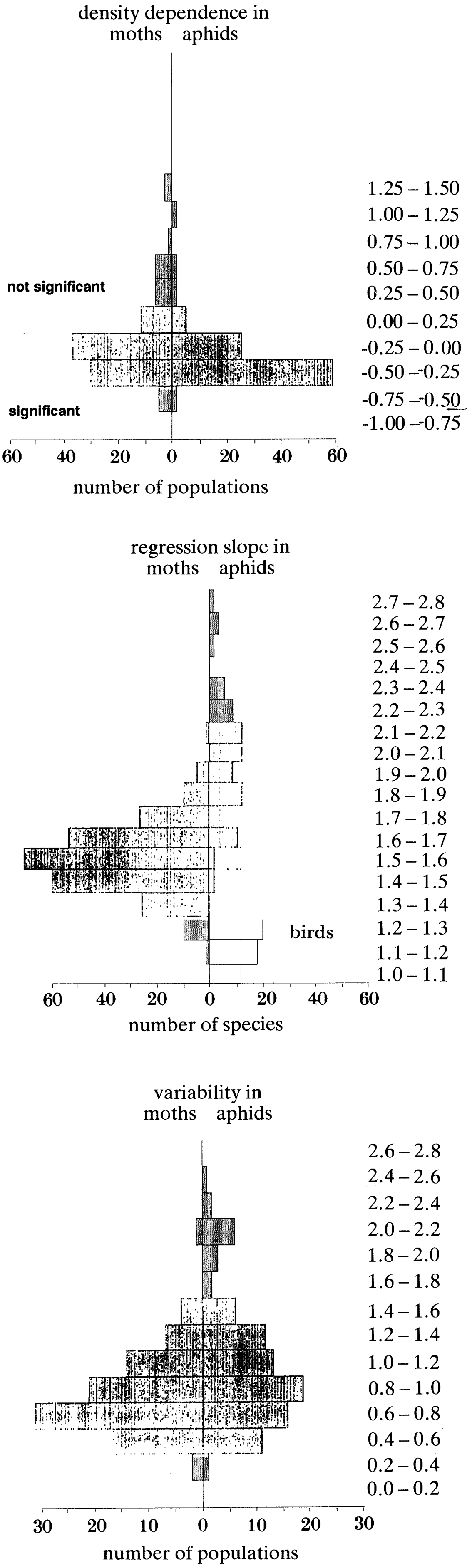
The comparisons in the previous sections suggested that terrestrial vertebrates tend to have more regulated and less variable populations than arthropods. In this section I will examine the relations between density dependence, regulation and variability in 10 species of moths and 10 species of aphids, each species sampled for an average of 16 years at about 10 localities distributed throughout the United Kingdom, yielding a total of 190 time series. (The data are from the Rothamsted Insect Survey (Taylor 1986); a more comprehensive analysis will be published with I. Woiwod.)

Density dependence of population change was tested using two methods, an extension of the Ricker equation (Turchin 1990; delayed density dependence) and Bulmer's (1975*a*) autoregressive method (statistic R, direct density dependence). Turchin (1990) found a significant delayed effect in 8 out of 14 forest insects. In the 190 time series for British moths and aphids, there were 10 significant ($p < 0.05$) coefficients for the delayed effect, just the number expected by chance. The striking contrast between this result and Turchin's (1990) result is probably because many of the well-studied forest insects are outbreak species or have cyclic dynamics. In contrast, the evidence for direct density dependence in British moths and aphids is overwhelming: significant density dependence was found in 73 and 92% of the moth and aphid time series, respectively (figure 3). There was significant variation in the degree of density dependence between species but not between localities. These results show a higher incidence of density dependence than reported in most previous surveys. A possible explanation is discussed in the next section.

We are now ready to turn to the relations between density dependence, population regulation and variability. Theoretical considerations suggest that generally there is no simple relation between density dependence and variability, but assuming that populations have a stable equilibrium point, we would expect species with stronger density dependence to show less variability than species with weaker density dependence. Such a relation is found in moths but not in aphids (figure 4). This result suggests that aphid populations are not generally regulated towards a stable equilibrium point. Turning to the relation between the average level of variability and the degree of density dependence of variability, we find that they are negatively correlated in both moths and aphids (figure 4). This correlation parallels the result from the comparison between vertebrates and arthropods, and suggests that the more regulated populations tend to be less variable.

(*d*) *Density dependence of density dependence*

The frequent failures to detect significant density dependence in empirical studies may be explained by the methodological problems enumerated in §2*a*, but there is also an interesting biological possibility. Many population studies have been conducted on common species with tendency to outbreaks. Latto (1989) found that of the 63 insect life table studies quoted in Stiling (1988) and Hassell *et al.* (1989), 40 studies (63%) were of species that can clearly be called 'pests'. Turchin's (1990) observations on frequent delayed density dependence in forest insects suggest that many of these best-known population studies involve outbreak species, in which density dependence may occur less



constantly than in many less common species, or which may have otherwise more complex dynamics than most uncommon species, making detection of density dependence more difficult. Ironically, detecting density dependence may be especially difficult in the kinds of species that are most frequently studied by population ecologists!

Additional support for this suggestion is given by the high incidence of density dependence in 'ordinary' (non-outbreak) British moths and aphids (figure 3), and by the observations that among these 'ordinary' species, density dependence of population change becomes less obvious, and density dependence of variability decreases, with increasing average density (table 3; the latter result has been previously reported by Hanski (1982) and Taylor & Woiwod (1982)). In summary, our fascination with outbreak and cyclic species may seriously bias our understanding of population dynamics in the vast majority of species.

3. MULTI-SPECIES TIME SERIES

(*a*) *Constancy of species composition*

A simple classification of communities may be based on the average level of variability (s) in the species, and on the concordance of their temporal abundance changes, measured by the average value of pair-wise rank correlations (r) in figure 5. The four 'ideal community types' of Strong *et al.* (1984) occupy the four corners in this scheme, with the caveat that their type (iii) may show high or low correlation. Ecologists have speculated on the mechanisms that are likely to dominate in the different kinds of communities. Correlated abundance changes have been assumed to imply the operation of some 'deterministic' factors, particularly interspecific competition (Grossman 1982; Strong *et al.* 1984); low correlation and low variability have been assumed to characterize species assemblages with independently regulated populations (Strong *et al.* 1984); while the combination of large variability but low correlation suggests the operation of strong environmental stochasticity (Strong *et al.* 1984). Although such inferences about population dynamic processes based on variability and interspecific correlation have only heuristic value, I shall advance some new suggestions below.

Figure 5 shows the position of 14 north temperate and boreal insect and vertebrate communities with

Figure 3. Comparison of British moths, aphids and birds in density dependence of population change, density dependence of variability and in the level of variability. Density dependence was measured by using Bulmer's (1975*a*) R (the values shown are R–R_c, where R_c is the lower 5% point of R; negative values thus show significant density dependence at 5% level). Density dependence of variability was measured by the slope of the variance–mean regression as explained in the text. Variability was measured by s, the standard deviation of log-transformed abundances. The regression slopes are from Taylor & Woiwod (1980, 1982). Calculations of density dependence and variability were done on 190 populations of 20 species of moths and aphids (data from the Rothamsted Insect Survey).

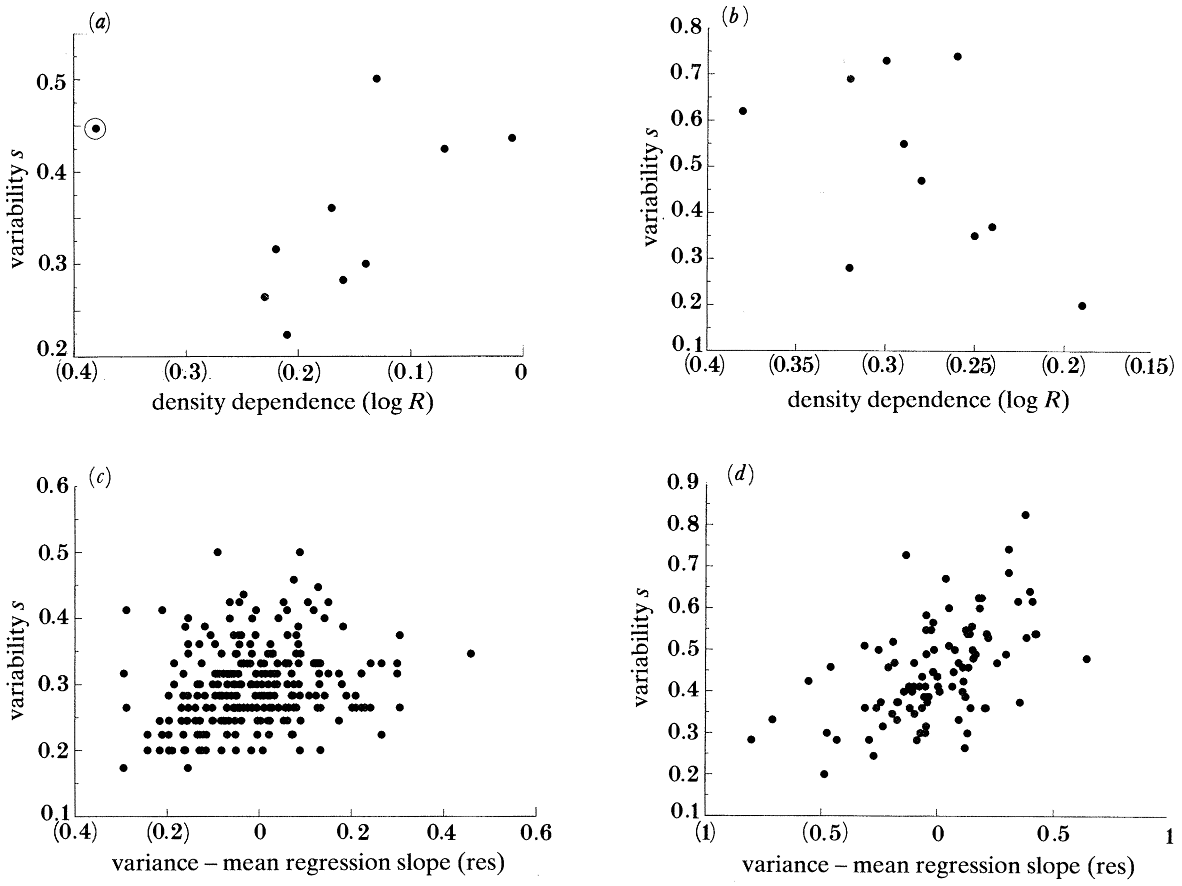


Figure 4. Relations between density dependence of population change and variability, and between the temporal variance–mean regression slope and variability, in British moths (*a*), (*c*) and aphids (*b*), (*d*). Density dependence was measured by using Bulmer's R (note that density dependence increases with decreasing log R). To remove the effect of mean density on the regression slope (cf. table 3), I first regressed the slope against the mean, and used the deviation from this regression line instead of the value of the slope. Statistics: (*a*), $r = 0.71$, $p < 0.05$ (excluding the circled migrant species, *Plusia gamma*); (*b*), $r = -0.52$, $p = 0.10$; (*c*), $r = 0.39$, $p < 0.001$; and (*d*), $r = 0.51$, $p < 0.001$. Data: variability and the regression slope from Taylor & Woiwod (1980); density dependence is the average value for 10 species sampled at about 10 localities throughout the United Kingdom (data from the Rothamsted Insect Survey).

Table 3. *The relations between density dependence of population change (Bulmer's R) and abundance, and between density dependence of variability (temporal variance-mean regression slope b) and abundance, in British moths*

(Results on density dependence are based on 98 populations of 10 species (data from the Rothamsted Insect Survey). Results on variance-mean regressions are based on the 263 species reported in Taylor & Woiwod (1980). t is the t-test value of the regression slope.)

	dependent variable: abundance			
independent variable	t	sign.	n	R^2
Bulmer's R (density dependence)	3.13	0.002	98	0.10
slope b (regulation)	11.74	<0.001	263	0.35

respect to interspecific correlation and variability. The bird assemblages are characterized by high correlation but low variability; the insect communities have high variability and high correlation; while small mammals display the highest level of variability and the greatest spread of correlations (figure 5). The combination of low correlation and high variability has been suggested to show strong environmental stochasticity, but the temperate small mammals present a counter-example: their cyclic populations show strong but delayed density dependence, and the low average correlation is due to different species participating to different degrees in different peaks of the multiannual cycle (Henttonen 1986). Many temperate small mammals comprise an exception to the generally low level of variability in vertebrates (figure 2).

I suggest three tentative conclusions on the basis of figure 5. First, there are no communities with low variability and low correlation, which would suggest strong but independent population regulation in the species. Second, species in the communities with high variability and high correlation (insects in figure 5) are

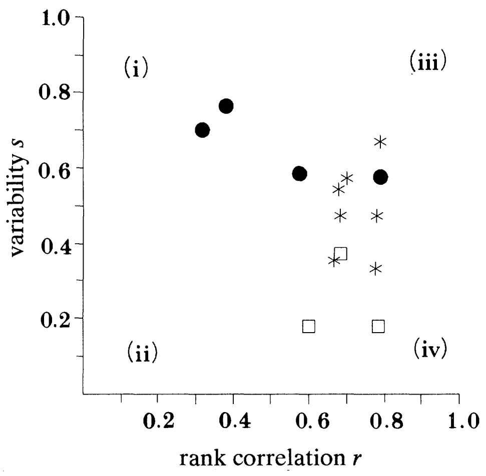


Figure 5. Position of 14 communities of north temperate and boreal insects (crosses), birds (squares) and small mammals (circles) with respect to the average of the Spearman's rank correlation between yearly abundances of pairs of species, and the average level of variability in the species. Variability was measured using annual census data, but in all cases shown here this measure is a good approximation of variability measured over generations. Data from Henttonen *et al.* (1987); T. Solonen (unpublished data); Skarén (1972); Vlasak (1987); Takeda (1987); den Boer (1977); Sheftel (1989); Doube *et al.* (1991); Ruszkowski *et al.* (1981); Sellin (1988); Enemar *et al.* (1984); Gilbert & Owen (1990); I. Woiwod (unpublished data).

affected by strong environmental stochasticity, with correlated effects on all or most species. And third, communities with low variability but large correlation (birds) are structured primarily by interspecific competition, while communities with high variability but low correlation (small mammals) are more affected by predation. It will be interesting to see what modifications to these conclusions are needed when more data of this sort are available.

(*b*) ***Statistical modelling techniques***

Autoregressive analyses of single-species data aim at revealing whether abundance changes are affected by density dependent processes, for instance intraspecific competition. If time series data are available for several interacting species, more complicated regression and other statistical models may be used to examine predator–prey and competitive interactions between two or more species (Bulmer 1974, 1975*b*; Teräsvirta 1982; Owen & Gilbert 1989). It is however debatable how strong inferences one may draw about interspecific interactions from such observational data. This is an area where experimental techniques are much preferable to analyses of observational data.

4. LIFE TABLE TIME SERIES

I suggested in a previous section that the interesting task for a population ecologist is not to show what is strongly expected, the occurrence of some density dependence, but to uncover the temporal and spatial scales, and the stages in species' life cycles, where density dependence occurs (Williamson 1972; Sinclair 1989). Following Varley & Gradwell (1960), hundreds of ecologists have regressed k-values against density (N_t) to detect the operation of specific density dependent mortality factors (the k-value is $\log[N_t/N_s]$, where N_s is the number or density of individuals which survived during the focal life stage).

There are several recent reviews of the incidence of density dependence in life table studies (Dempster 1983; Strong *et al.* 1984; Stiling 1987, 1988). These reviews purport to show that, contrary to what most ecologists would expect, 30–50 % of the original studies failed to find any density dependent factors at all (Dempster 1983; Stiling 1988), and where density dependence was detected, it was more often because of an upper 'ceiling' set by limiting resources rather than to natural enemies operating at all densities. By using the same data that were analysed by Stiling (1988), Hassell *et al.* (1989) showed how the percentage of studies in which density dependence was detected increases with the duration of the study, suggesting that many studies have been conducted over such short periods of time that conclusions about density dependence should be drawn with great caution.

Another particular issue which has been much debated recently is the relation between spatial and temporal density dependence. Hassell (1985) suggests that many populations may be primarily regulated by spatial ('within-generation') density dependence, and he argues that it may be difficult, given spatial heterogeneity and omnipresent stochasticity, to detect temporal, year-to-year density dependence by using conventional life table analysis. More recently, Stewart-Oaten & Murdoch (1990) have shown that spatial heterogeneity can indeed translate spatial density dependence into temporal density dependence, and thereby increase stability, but their model suggests that spatial heterogeneity is generally more likely to have a destabilizing than stabilizing effect.

The emphasis on spatial density dependence is welcome as it brings the issues to the level of individuals that actually experience and are affected by the lower or higher density. There is an increasing interest in ecology to replace phenomenological, population level theories and approaches by more mechanistic alternatives with clearly measurable quantities at the individual level (Tilman 1988; Lomnicki 1988). None the less, as far as population regulation is concerned, what matters is temporal density dependence (Mountford 1988). Population regulation by definition means changes in the overall population size within a finite range of values. What is meant by 'overall population size' is not self-evident, however, and is discussed in the next section, population regulation may occur at different spatial scales.

5. POPULATION, OR METAPOPULATION, REGULATION?

The previous sections have followed the prevailing paradigm in population ecology in discussing questions about population regulation and variability at the level of local populations. There is an alternative perspective in the literature, which emphasizes how 'a natural population occupying any considerable area will be made up of a number of ... local populations' (Andrewartha & Birch 1954), how 'the risk of wide fluctuation in animal numbers is spread unequally over a number of subpopulations', and how 'the consequences of this spreading of the risk in space will be a relative reduction in the amplitude of fluctuations of animal numbers in the entire population' (den Boer 1968). Following Levins (1969), the 'entire population', or the ensemble of local populations, is frequently called a metapopulation.

Much confusion has been created by the claim (den Boer 1968, 1987) that metapopulation regulation or persistence requires no density dependence at the level of local populations. The claim is incorrect. Without any density dependence, populations would grow indefinitely large, or they would go rapidly extinct, and in the latter case no metapopulation would persist for long. Density dependence is required for metapopulation persistence; what is not needed is regulation of local populations.

Two other requirements for metapopulation regulation, when local regulation fails, are dispersal between local populations, and asynchronous dynamics in these populations. Asynchronous local dynamics may be due to population dynamic factors, such as predator–prey interaction (Taylor 1988), or to stochastic environmental factors. Metapopulation regulation is likely to play the greatest role in species with large local variability but little synchrony among populations. Figure 6 shows that in 20 species of moths and aphids sampled throughout the United Kingdom, the species with more variable populations tended to have more synchronous dynamics. A positive relation between variability and regional synchrony suggests that high variability in these insects is largely because of regionally correlated environmental stochasticity, and not to local dynamics. Alternatively, the result in figure 6 could be because of a high level of dispersal among unstable (highly variable) local populations, but this explanation seems unlikely in the scale of the U.K. In any case, positive correlation between variability and regional synchrony is not favourable for metapopulation regulation in the face of weakly regulated local populations with high variability. It remains to be shown by future studies whether the pattern in figure 6 is the rule or the exception. More generally, it is yet a very open question how frequently species persist as metapopulations with unstable local populations (Taylor 1988; Harrison 1991).

In spite of the negative result for metapopulation regulation in figure 6, I cannot resist the temptation to speculate on a special group of species, but a group that may actually comprise the majority of species on Earth. I have in mind the arthropods which are living in the canopy of tropical forests. Given the tremendous diversity and patchy distribution of tree species in tropical forests, and the probably quite high (but unknown) frequency of monophagous and oligophagous insect species (Erwin & Scott 1980; May 1988), the canopy of tropical forests may well appear to many species like the classical metapopulation scenario as originally envisaged by Levins (1969): small and like patches of suitable habitat placed randomly in the matrix of inhospitable surroundings. To what extent are the immense numbers of canopy-living arthropods in tropical forests (Erwin & Scott 1980; Stork 1987; May 1988) regulated by metapopulation dynamics? To what extent is the coexistence of these species based on metapopulation dynamics? These are fascinating questions without even a hint of an answer.

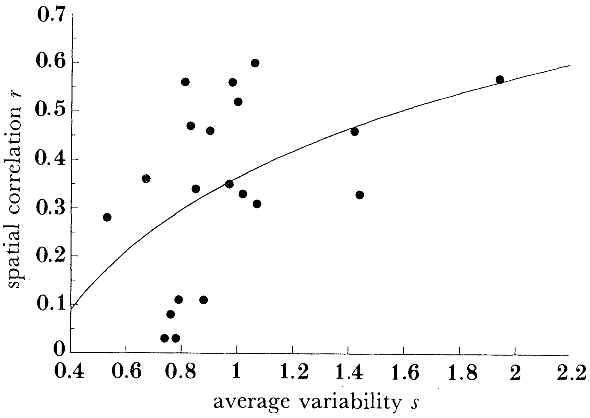


Figure 6. Relation between average local variability and average spatial correlation of population fluctuations (regional synchrony) in 10 species of moths and 10 species of aphids, each sampled at about 10 localities distributed throughout the United Kingdom.

6. CONCLUSION

The majority of population dynamic studies deal with common species, which have large local populations and are widely distributed, or species that have outbreaks at regular or irregular intervals. Our perception of density dependence, regulation and variability in animal populations is biased towards such species with perhaps especially complex dynamics. Directing more attention towards uncommon and rare species would be most welcome, because they represent the majority of species, but there remain formidable practical problems in estimating variability of rare species, and in showing at which spatial scale their populations are regulated.

I am most indebted to T. Solonen and I. Woiwod for making unpublished data available to me. Comments and suggestions by K. J. Gaston, J. Latto, W. W. Murdoch, A. D. Taylor, P. Turchin, I. Woiwod and X. Xia helped me greatly.

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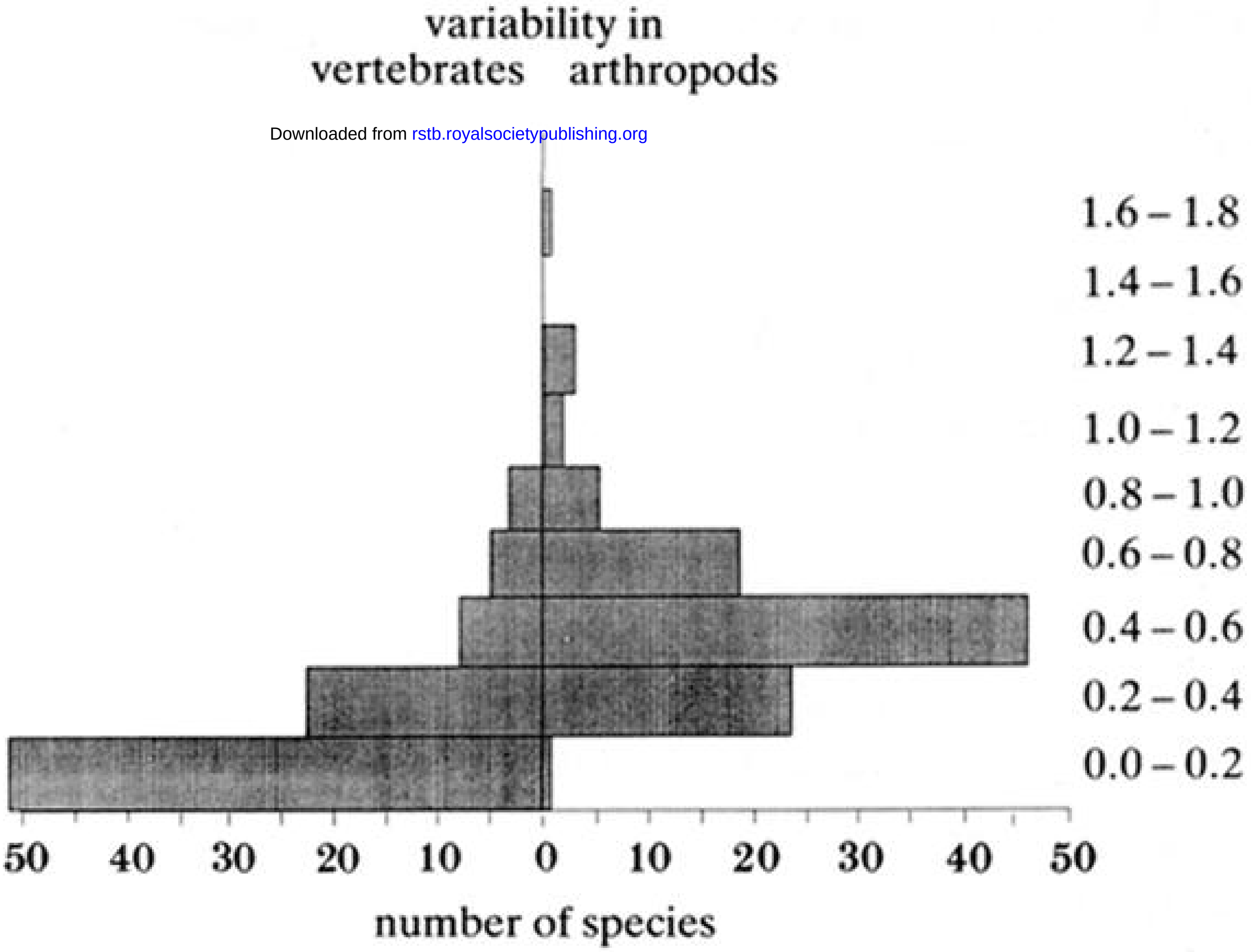

igure 2. Population variability (s) in 91 species of terrestrial ertebrates (mammals, birds and lizards, from Connell & ousa (1983); Schoener (1985); Ostfeld (1988); T. Solonen, npublished data), and in 99 species of terrestrial arthropods noths, aphids, hoverflies, grasshoppers, etc., from Connell Sousa (1983); Owen & Gilbert (1989); Joern & Pruess 1986); I. Woiwod, unpublished data). Variability has been neasured for generations where possible (most studies). The istributions for vertebrates and arthropods are highly gnificantly different (two-tailed Kolmogorov–Smirnov stattic 0.58, $p < 0.0001$). Note that average variability in the ve forest insects in figure 1 remains between 0.4 and 0.6, the nodal class for arthropods in this figure, for the time periods etween 5 and 30 years, which bracket the typical lengths of me series data available for most species. The results in gures 1 and 2 are thus consistent with each other.

igure 3. Comparison of British moths, aphids and birds in ensity dependence of population change, density depen- ence of variability and in the level of variability. Density ependence was measured by using Bulmer's (1975*a*) R (the lues shown are R–R_c, where R_c is the lower 5% point of R; egative values thus show significant density dependence at % level). Density dependence of variability was measured the slope of the variance–mean regression as explained in e text. Variability was measured by s, the standard eviation of log-transformed abundances. The regression opes are from Taylor & Woiwod (1980, 1982). Calculations density dependence and variability were done on 190 opulations of 20 species of moths and aphids (data from the othamsted Insect Survey).