To the Graduate Council:

I am submitting herewith a dissertation written by Andrew Redfearn entitled "Population Stability in Animals." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

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POPULATION STABILITY IN ANIMALS

A Dissertation

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Degree

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Andrew Redfearn

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Academic Press kindly allowed me to use my chapter (pp. 99-133) in the book "Insect Outbreaks" (P. Barbosa, and J.C. Schultz, eds.) for section II of this dissertation. The Ecological Society of America kindly allowed me to use my article published in "Ecological Monographs" (vol. 58: 39-55) for section III of this dissertation.

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ABSTRACT

This dissertation contains five sections. Section I is an introduction.

Section II of this dissertation has been published in the book entitled "Insect Outbreaks" edited by P. Barbosa and J.C. Schultz (Redfearn and Pimm 1987). Section III has appeared in "Ecological Monographs" (Redfearn and Pimm 1988). Section IV will be published in an Oak Ridge National Laboratory Technical Memorandum entitled "Recent Advances in Food Web Theory" edited by D.L. DeAngelis (Redfearn and Pimm, in press). Section V will appear in "Nature" (Pimm and Redfearn, in press).

In section II I show that the application of insecticidal sprays causes an increase in the rate of population growth of certain insect pests.

In section III I report that variability in population density through time may be lower in herbivorous insect species that feed on a wide range of host plants than in species with a narrower diet. Other authors have reported the opposite result.

Section IV also examines temporal population variability. This section reviews the literature on temporal population variability. I recognize three kinds of factors that may affect variability: environmental factors, community effects, and the intrinsic properties of the species. I show that body size is negatively correlated with variability.

In section V I report that estimates of temporal population variability increase as we include more years of data in those estimates. This is consistent with the idea that time series of population densities have reddened spectra: high amplitude fluctuations in density occur less frequently than low amplitude fluctuations. Major changes in numbers are rarer than minor changes.

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I. GENERAL INTRODUCTION

Two measures of population stability are resilience, or the rate that populations return to some 'equilibrium' or average density after having been perturbed from that density, and population variability, the extent to which population densities change through time (Pimm 1984a).

In section II of this dissertation I review various definitions of population stability and of community complexity and I discuss their relevance to the study of insect outbreaks. In particular, I examine the relationship between resilience and the number of trophic levels within insect communites.

1. THE NUMBER OF TROPHIC LEVELS AND RESILIENCE

We might usually equate resilience with stability: the greater the resilience, the faster the system recovers following some reduction in numbers. But consider an insect pest population

increasing towards some high density that involves far more pests than we would like. By definition, a species with a resilient population will reach that level faster. Population resilience can thus be a measure of instability and also a measure of how frequently we must control the insect by chemical means. In section II of this dissertation I ask, How does food chain length modify a species' resilience?

Pimm and Lawton (1977) used Lotka-Volterra models to construct food chains of varying length. They found that the constituent species in long food chains took a relatively long time to return to equilibrium levels following a disturbance. Short food chains were highly resilient. Removing trophic levels will mean that pest outbreaks will occur faster. One way of removing trophic levels is by applying insecticides. These clearly kill many pests, but many predators are killed as well. The predators, moreover, require that the pest returns before they themselves can recover.

Thus, there will be a 'time window' following insecticide applications when the pest has relatively few predators. Food chain lengths are effectively shortened. This suggests that the application of insecticides should cause an increase in resilience in the pest population.

I searched the literature for studies which estimated insect pest population levels after an insecticidal application, and which compared these levels to those in a nearby untreated population. Almost all populations treated with sprays increased at a higher rate than the corresponding untreated population. Thus, by removing predators, the application of insecticidal sprays appears to increase resilience. Removing trophic levels does increase the resilience of the remaining populations.

2. VARIABILITY

Sections III, IV and V of this dissertation examine a second measure of stability: variability, which I define as the extent to

which the density or number of individuals in a given population fluctuates from year to year. Variability can be measured by such statistics as the coeficient of variation of density (CV) and the standard deviation of the logarithm of density (SDL) (Williamson 1972).

Why is variability important? First, variability has relevance to conservation and pest management. High variability results in a high probability of a population becoming exceptionally rare, and thus in danger of extinction. Alternatively, it may lead to a high probability of becoming exceptionally abundant, and thus perhaps becoming a pest. High variabilities may also lead to difficulties in predicting abundances, and thus to difficulties in the management of the population. Second, variability is just one measure of population stability and so has obvious relevance to such theoretical issues as the relationship between stability and community complexity (Pimm 1984a). It also has relevance to the question of whether ecological equilibria exist in nature. The more variable a population, the more likely we are to

reject the equilibrium view.

Population densities change from one year to the next for a variety of reasons. The favorability of the climate changes through time. Densities of other species, such as competitors, predators and prey, change. These changes may be unpredictable or predictable in nature. Changes in population density due to climatic changes are generally unpredictable. Populations may show trends, limit cycles or more complex chaotic behaviours which are all predictable in nature (Schaffer and Kot 1986). The definition of variability that I use does not distinguish the possible causes of population change; nor does it separate predictable and unpredictable changes. For example, a population showing limit cycles will, according to my definition, be somewhat variable, even though the changes in density are predictable. My definition of variability is a purely operational one. The results that I shall present in sections III, IV and V may well be improved or altered by removing the predictable components of population change (trends, cycles, chaos) and examining the residual unpredictable

components of variability. Distinguishing and separating the components of variability require very long term data sets, but this is work that I will be involved with in the future.

There are at least three sets of factors that may affect variability: the variability of the abiotic environment, food web effects, and the intrinsic properties of the species.

Highly unpredictable, variable environments tend to be characterized by highly variable populations (Malicky 1976, McGowan and Walker 1985) but comparisons between populations in different environments tend to be flawed by the fact that different species are compared in the different environments. Each set of species is likely to be uniquely adapted to the special selective pressures imposed on them, by their respective environments.

Food web effects have also been examined by comparing the population variabilities of species in different systems. Different systems are assumed to be characterized by food webs of different degrees of complexity. Such comparisons have been made to test Elton's (1958)

and MacArthur's (1955) assertion that simple systems are less stable than complex ones. Complex tropical forest systems do not appear to be composed of especially stable populations compared to relatively simple temperate forest systems (Wolda 1983), but extremely simple agricultural systems do appear to be characterized by highly variable populations (Wolda 1983, Rejmanek and Spitzer 1982). These systems differ in ways other than just food web complexity, however.

An alternative way to explore the role of food web structure is to compare species within the same community and ask: are species that interact with many other species more, or less, variable than species that interact with few other species?

In herbivorous insects, for example, we can look at the effects on a species' population variability of the number of species with which it competes, the number of host plant species on which it feeds, and the number of species of predators and parasites that attack it. Competition is thaught not to be an important

process structuring herbivorous insect communities (Strong et al. 1984) and so in section III of this dissertation I look at the effects relating to host plants. The effects relating to natural enemies will be examined in the future.

3. THE DEGREE OF POLYPHAGY AND VARIABILITY

In section III of this dissertation I ask, how does the range of host plants a given species exploits affect its variability. MacArthur (1955) argued that polyphagous species have a greater choice of energy sources than host-specific species, and so if one host species has an abnormal abundance, this should have a relatively small effect on the polyphagous species' abundance.

The extreme case of a host species going extinct will inevitably lead to the extinction of a monophage dependent on that one host species. A polyphage can obtain energy from other sources. This argument therefore suggests that populations of host-specific species should be more variable

than those of polyphagous species.

Watt (1964, 1965, 1973), however, analyzed data on Canadian forest moths and found the opposite result. Polyphagous species were the most variable. Watt suggested that this was because a polyphagous species has a greater amount of available habitat in a given area. Hence, during favourable years, polyphagous species should spend less time searching for suitable host plants, reproduction rates should be higher, and the populations should increase to higher levels than those of monophagous species.

In order to evaluate these two alternative arguments, I analyzed data on British aphids and moths, and reanalyzed Watt's data on Canadian forest moths. I found no evidence that polyphagous species are more variable. Where there was a significant effect of polyphagy, it was a negative one: polyphagous species were less variable, as MacArthur's argument predicts. I do not wish to rule out Watt's argument, however. Rejmanek and Spitzer (1982) showed that, in south Bohemian Noctuid moths, polyphagous species were the most variable.

All of these results on polyphagy suggest that changing resource levels may cause fluctuations in abundance, the magnitude of which being modified by the range of host plants exploited. There is, however, a widely held view that regulation by predators and parasites is more important in herbivorous insect populations than is regulation by resources (Strong et al. 1984). We may thus expect an even stronger effect of natural enemies on variability. I intend to examine this effect in the future.

4. BODY SIZE AND VARIABILITY

In addition to environmental and food web effects, the intrinsic properties of the species may be important in determining population variability. In section IV of this dissertation I concentrate on the effects of the body-size of the species on variability. Using a data set comprising insects, birds and mammals, I show that large bodied species are generally less variable than small bodied species. The reason for this correlation is uncertain but it may be

due to the direct effects of body size on variability, small bodied species being more succeptible to inclement weather (Lindstedt and Boyce 1985). Alternatively, it may be due to the indirect effects of confounding factors. For example, small bodied species may be more variable because they tend to have high reproductive rates (Southwood 1981). There is a good argument for a positive relationship between reproductive rates and population variability (May et al. 1978).

5. VARIABILITY AND THE LENGTH OF THE CENSUS

In section V I show that measures of variability of a given population increase as we increase the number of years included in those measures. This result is consistent with the idea that time series of population densities have reddened spectra. The amplitude of population changes increases with the period of those changes. Major changes in density are rarer than minor ones.

Steele (1985) and Williamson (1981, 1987)

have argued that physical variables such as atmospheric temperature show reddened spectra too. If this is true, and if physical variables force variability in populations, then this would explain why populations show reddened spectra.

This result has implications for questions about the nature of ecological equilibria. Density dependent factors may set an average or equilibrium density over a short period of time. But this equilibrium level may cycle over longer periods, and that cycle mey, in turn, be moving on an even more powerful, infrequent cycle.

II. INSECT OUTBREAKS AND COMMUNITY STRUCTURE

1. INTRODUCTION

(a) Approaches and Purposes

Understanding pest outbreaks is likely to come from considering them at a number of levels. Certainly, detailed understanding of a particular outbreak must come from studying the particular species involved. But studying individual species is an abstraction: no species exists in isolation from all the other species in its community. While it will be impossible to study all the species in a community in any detail, we can examine broad community- or ecosystem-level features for correlates of outbreaks. The information such examinations might yield will be quite general, but it still may be useful in suggesting strategies for particular systems.

I shall take both theoretical and empirical approaches in this chapter and examine the patterns of trophic interactions and their effects on community stability. In particular, I shall consider whether instability is promoted by

the simplification in plant and animal communities caused by our planting crops in near monoculture.

I have two purposes. First, I hope to clarify the confusion stemming from the various meanings of the word 'instability' and so bring existing literature into clearer focus. Second, I hope to find those theoretical approaches that might provide fresh insights. There is no guarantee that theory will prove useful, so I shall try to point to field studies that seem best explained by the theories that have been developed.

(b) The Meanings of 'Instability'

Both Elton (1958) and MacArthur (1955) argued forcefully that there might be a relationship between a population's dynamics and not just the intrinsic properties of the species, but those of the community to which it belongs. Both attributed instability to system simplicity. Elton argued that pest outbreaks were just one of many manifestations of instability and that they were more likely in simple, agricultural systems than in complex, natural systems. And he relayed

a conversation with some tropical foresters that (perhaps mistakenly) led him to believe that pest outbreaks are a feature of simple, temperate forests but not of complex, tropical ones.

MacArthur developed his ideas somewhat more formally. He defined instability in these terms:

'Suppose, for some reason, that one species has an abnormal abundance, then we shall say that the community is unstable if the other species change markedly in abundance as a result of the first. The less effect this abnormal abundance has on the other species, the more stable the community.'

MacArthur defined the correlate of stability, complexity, as 'the amount of choice of the energy in going through the (food) web.'

It is tempting to be highly critical of these early studies. Elton's arguments are heterogeneous and often based on scant evidence. Agricultural systems differ in many ways from natural ones and there are some remarkably simple natural systems that are not devastated annually by insect herbivores. (Examples include the large stands of bracken fern, Pteridium, studied

extensively by Lawton (Strong et al. 1984 is a review.).) MacArthur's argument is fine as it stands, but is incomplete: it considers changes in abundance of species at the base of food chains. Changing abundances of top predators might (and indeed does) have the opposite effect: the more complex the web, the more widely disturbances may propagate. Yet I consider these early studies to be particularly important. They argue that examining the characteristics of a single species is not enough: we must look at the system to which it belongs. They also point to a wide variety of possible meanings, not just of instability, but also of community features that may correlate with instability.

Clearly, what I must do first is to look at the various definitions of population stability. Then I will ask these questions: 1) to what extent do the various kinds of instability correspond to pest outbreaks? 2) How do these kinds of instability vary with the properties of system to which the species belong? 3) Is there any evidence that outbreaks are more likely in systems with certain trophic structures, simple

ones for example?

In reviewing the meanings of 'stability', Pimm (1984a) has recognized five major ideas: stability (in the strict, mathematical sense), resilience, persistence, resistance and variability.

Stability A system is deemed stable if and only if the species' densities tend to return to their equilibrium values following disturbances to the densities. In a variable, uncertain world, equilibrium levels may not be the population levels where species remain; in such cases, equilibrium is better defined as the level below which the population tends to increase and above which the population tends to decrease (Tanner 1966, Pimm 1984b).

Resilience measures how fast a population returns to equilibrium. Resilience is measured in models by the characteristic return time; the time taken for the perturbation (equilibrium density minus the population density) to fall to 1/e (ca 37%) of its initial value. A resilient system has a short return time.

Persistence measures the time a system lasts

before it is changed to a different one; for example, how long a system may last before one equilibrium is replaced by another. Resistance is the tendency for a system to remain unchanged by a disturbance.

Variability includes such measures as the variance, standard deviation or coefficient of variation of population densities over time.

Stability (in the strict mathematical sense), resilience and variability seem most relevant to the topic of pest outbreaks and it is these that I shall consider in the remainder of this chapter.

2. STABILITY

(a) The Stability-Complexity Question

Stability is well defined mathematically and most theoretical studies examine it alone. Early studies (such as those of Gardner and Ashby 1970 and May 1972) found that a smaller proportion of models of multi-species systems were stable when there were more species, when a greater proportion of those species interacted (high connectance) and when the species interacted more

strongly. This seemed so contradictory to the notions of Elton and MacArthur that considerable efforts were made to evaluate the many unrealistic assumptions these early models required. The patterns of the interactions were made more realistic, so were the parameters and even the form of the equations. (Some reviews of this literature are given by May (1973, 1979) and Pimm (1982, 1984a); to give their details here would be repetitious.) The initial results, however, were, to a large extent confirmed by the more recent analyses. Complex models were less likely to be stable. The results can be most easily reversed by using models in which the predators have no effect on their prey's population growth rate (so-called 'donor-controlled' models) (DeAngelis 1975). This can happen, for example, if predators take those prey that are most likely to die from other causes--starvation, for example. There is a large literature on removing predatory species from communities or, as in the case of biological control, introducing them. If predators have no effect on the population dynamics of their prey,

we would expect the removal or addition of predatory species to have no impact on the remainder of the food web. Pimm (1980) examined 19 previously published real food webs from which a predator was removed. Only four systems did not lose species following the removal. Furthermore, the impact of biological control agents can be very large, with insect predators, for example, depressing prey populations to a fraction of one percent of the levels in the predator's absence (Beddington et al. 1978). In short, the donor-controlled assumption does not seem to be a good one. The vast majority of studies show that predators do have an impct on the densities of their prey. And so we are faced with the conclusion that more complex systems are less likely to have a stable equilibrium than simple ones.

On closer inspection, this conclusion does not contradict the ideas of MacArthur and Elton as much as it might superficially appear (Pimm 1982, 1984a). There is no difficulty with the idea that systems with stable equilibria are likely to persist. Those with only unstable

equilibria can have one of two initial fates: they can lose species and settle to a new stable equilibrium; or the populations may persist, oscillating probably in some complex manner. For many natural systems these two initial fates are really the same: large amplitude oscillations will eventually mean that populations will be driven to such low levels that they will not be able to recover. Thus, stable systems will persist, while unstable systems will tend to lose species and simplify to the point where they will contain a stable species assembly. The systems we see in the real world should be stable.

While the quantitative results of stability analyses depend on the various assumptions used, there is a qualitative prediction that seems relatively robust: to retain stability, the product of two measures of community complexity, species number (n) and connectance (C), should be smaller than a critical value (which depends on the strength of the species interactions). If the systems we observe in the real world are those that are stable, then observed values of C and n should fall in a region <u>below</u> a hyperbolic

function, as suggested by Fig. 1a. Data from a variety of communities, including the aphid-dominated systems shown in Fig. 1b, show this to be the case (Rejmanek and Stary 1979). What this shows is straightforward: the systems we observe in nature are relatively simple ones. There is now considerable evidence that the patterns of trophic interactions we observe in nature are simpler, in a variety of different ways, than we would expect by chance (Pimm 1982). There seems to be no reason to expect that simple crop ecosystems should not be stable.

(b) Species Deletion Stability

i) Introduction and model results

What happens when we simplify a system, say by reducing the number of species present? How often are we likely to retain a stable system and how often will the system become unstable (Fig. 1c)? Simple systems may often be stable, but there is no guarantee that we will produce stable systems from simplifying existing stable, complex ones. Answering these questions requires an examination of what Pimm (1979a) has called 'species deletion stability'.

Figure 1. Connectance, species number, and stability. (a) Values of connectance (C) and species number (n) that lead to stable and unstable systems in food web models. This result suggests that natural systems should have values of C and n bounded by a hyperbola. (b) Four hyperbolic approximations and the observed values of C and n for aphids, their plant hosts and their parasitoids. Discovered trophic connectance (●) was calculated on the basis of just the discovered interactions while potential total C (+) also includes all potential competitive interactions. After Rejmanek and Stary (1979). Reprinted by permission from Nature, Vol. 280, No. 5720, pp. 311-313. Copyright (c) 1979 Macmillan Journals Limited. (c) When species number is reduced, it is possible that the resultant system is unstable, even though, other things being equal, simple systems are more likely to be stable.

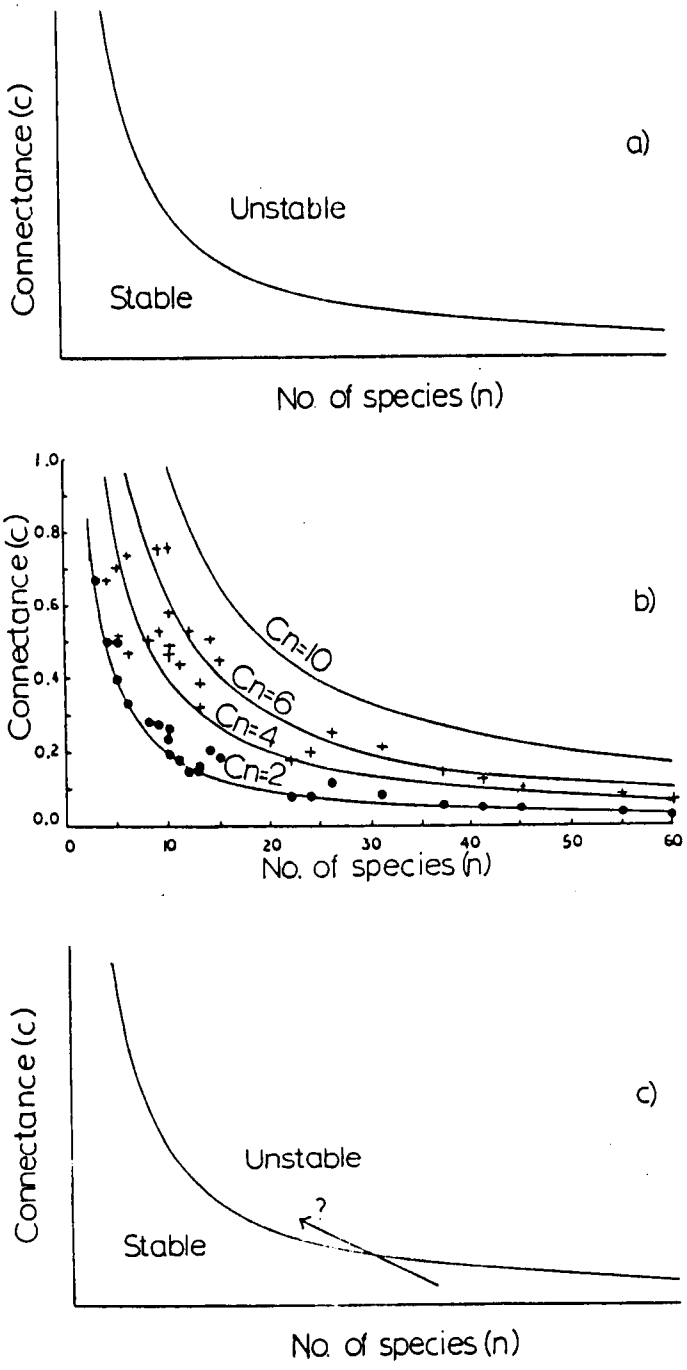
Connectance (c)
a)
Unstable
Stable
No. of species (n)
1.0
0.8
0.6
0.4
0.2
0.0
Connectance (c)
b)
Cn=10
Cn=6
Cn=4
Cn=2
0
10
20
30
40
50
60
No. of species (n)
Connectance (c)
c)
Unstable
?
Stable
No. of species (n)

Figure 1

A system is deemed 'species deletion stable' if, following the removal of a species, the remaining n-1 species can all coexist at a new, stable equilibrium (Pimm 1979a, 1980). We can determine a system's species deletion stability repeatedly for the same species and the same model structure but over ranges of interaction parameters designed to mimic those found in nature. This gives a probability of species deletion stability for that species' removal and for that particular web. These probabilities, averaged over all the species in a food web vary in much the same way with connectance, species number and interaction strength as does simple stability. The more complex the model community, the more likely a loss of a species will cause further species losses. Most model systems with complexities anything near those observed in nature are not species deletion stable; nor are natural systems. The vast majority of natural systems cannot withstand species removals without changes in species composition. (A review of this literature is Pimm 1980.)

From these studies it might seem we have an explanation of pest outbreaks in accord with the views of Elton and MacArthur: instability is caused by simplification (rather than just by simplicity). This may be so, but on close inspection it is not anywhere near so clear-cut as it might seem. Species deletion stability varies markedly depending on which species are removed from a community (Pimm 1980). The reviews of species removals mentioned earlier tend to focus on the removals of predators or top-predators. For these we expect, and find, further species losses. But for plant removals, particularly those of plants fed upon by generalized herbivores, models predict fewer losses. Moreover, these losses should become less likely, the more complex the system. There is less evidence to support this result. But one cannot help notice the lack of an effect of removing Chestnut, Castanea dentata, (Marsh.) Borkh, trees from eastern North America. Chestnuts occupied over 40% of the canopy in some areas in the early 20th century and have now almost totally disappeared (Krebs 1978). While

the disappearance may have caused the loss of Chestnut monophages, effects regarding this do not appear to have been recorded. In fact, there do not seem to have been any losses of vertebrate species.

The simplification practiced in agriculture leads me to ask a specific question: how often does the removal of an unwanted plant species cause the crop species' load of insect herbivores to increase? Thus, in reducing the competitors of the plants we wish to harvest, do we make the the crop species more vulnerable to attack by insects? This can certainly happen theoretically. A simulation is shown in Fig. 2. Here, the removal of a plant causes the loss of a generalist predator on a specialist herbivore: the remaining plant species goes to a lower equilibrium than before. But the models do not tell us how frequent this occurrence is in practice; it is certainly not inevitable, and it may be unlikely. Common sense dictates the conditions under which it will be a likely event: it will be when we remove plant species that are essential to the survival of generalist predators

Figure 2. The effect of removing a plant species (D) on the densities of the remaining species in the system. Note that the other plant species (A) may end with lower densities, because of the increased attentions of its herbivore (B).

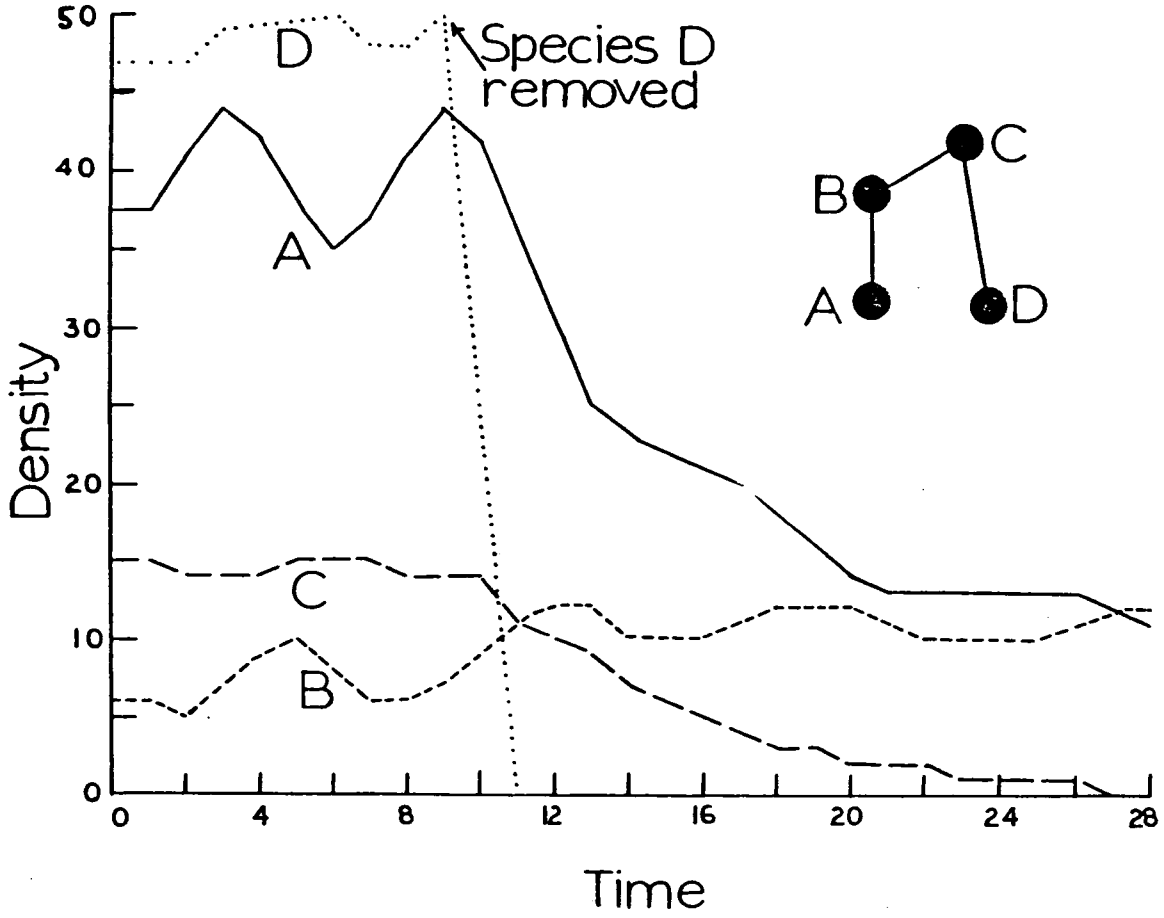
50
40
30
20
10
0
Density
D
Species D
removed
A
C
B
0
4
8
12
16
20
24
28
Time
C
B
A
D

Figure 2.

which have a controlling effect on the herbivores that feed on the crop (just as in Fig. 2). Moreover, the loss due to these herbivores must be greater than the gain obtained from competitive release.

In short, taking an existing system and simplifying it by removing species will usually cause further species losses. But it is far from certain that removing one plant species will cause a decrease in the other remaining plant species by increasing their vulnerability to insect herbivores. How do these results match our observations and intuition about the real world?

(ii) Review of field studies

The kinds of studies which have tested the ideas on simplification asked: how do insect numbers of a crop differ if that crop is grown singly, or in a multi-species planting. Root's (1973) study is an early example of such an experiment. Brassica were grown in a single-species planting and also among many other plant species. In multi-species plantings, more species of insect were present throughout the

planting and, on the Brassica itself, insect herbivores did not reach such high levels. From this, we might conclude that simplification caused a pest outbreak. But how general is this result? And exactly what is being simplified?

To answer these questions requires many other studies. Over 150 of them have been compiled in a timely and important review by Risch et al. (1983). In a highly significant proportion of cases, insect herbivores were more likely to reach high densities in single-species plantings. But there were some important patterns of variation.

Risch et al. (1983) argued that increased density in single-species plantings might be due to one of two causes. First, reduced predator diversity and impact might make herbivore outbreaks more likely. The second proposed cause was based on the phenomenon described in the 'resource concentration hypothesis' (Root 1973). The plants associated with the crop in a multi-species planting might have a direct effect on the ability of insects to find and utilize the crop. These associated plants may mask the

herbivore's host-finding stimuli, generally reduce movement between individual plants, or in various other ways, lower herbivore colonization rates.

The two hypotheses make different predictions about the effects of plant diversification on monophagous and polyphagous herbivores. Both groups might be expected to suffer from the increased attentions of predators in multi-species plantings, if this is the cause of the reductions in densities. But monophagous species should decline far more than polyphagous species, if the 'resource concentration' hypothesis is correct, because for polyphages the multi-species plantings will not represent such a dilution of resources.

The data support the 'resource concentration hypothesis'. For monophagous species, 61% of studies showed a decrease in density with multi-species plantings, 10% an increase and the rest were equivocal. For polyphagous species, 27% of the studies showed a decrease and 44% an increase. The differences were highly significant.

Risch et al. (1983) also went on to consider the differences between herbivores on annual and perennial plant species. They argued that annual species might rely more on escape in time from their herbivores, while perennials might rely on chemical defenses to slow herbivore growth. For the latter, herbivores would be subject to longer periods of exposure to predation. If the reduced numbers in multi-species plantings were due to the effects of predators, then we might expect differences between annuals and perennials. They were unable to detect such an effect. Thus, monophagous herbivores were less abundant in diversified plantings of annuals in 58% of the cases, and 67% of the cases for perennials. For polyphagous species, the corresponding percentages were 27 and 28.

In short, Risch et al. (1983) make a persuasive case that complexity reduces herbivore densities. But the complexity is that of the plant species and the physical effects spacing plants might have. It seems to have little to do with the trophic structure of the insect communities.

(c) Summary

Early ideas suggested that pest outbreaks in agricultural systems might be due to simplifying the system. Later theoretical studies suggest that there is nothing inherently unstable about simple systems. Indeed, it is sufficiently complex systems that should be unstable. We might expect such systems to simplify through species losses. The result should be that the systems we observe in nature are those that are relatively simple compared to what chance dictates (Fig. 1a). This seems to be the case.

Models show that the actual process of simplifying a system by removing species from it may be expected to cause further species losses and changes in the densities of the remaining species. Removal of plant species can lead to increased herbivore levels on some of the remaining plant species. But this is not inevitable. There is now a large collection of studies that show the effects on insect herbivores of simplifying a system by removing plant species. The insect herbivores are

generally more abundant on plant species grown in monoculture. But this seems to have far more to do with the difficulty of getting from host plant to host plant in the multi-species planting, than to any trophic interactions.

3. RESILENCE

(a) Does Insecticide-Use Increase Resilience?

How fast species' densities recover after a perturbation is a measure of stability that permits easy comparisons among existing systems. We might usually equate resilience with 'stability': the greater the resilience, the faster the system recovers following some reduction in numbers. But there is an interesting twist to this argument for pest outbreaks. Let us consider a pest population increasing towards a high density that involves far more pests and far too few of its hosts for our liking. A species with a resilient population will reach unacceptably high levels faster, is more likely to oscillate, and is numerically more likely to get away from its predators than a species that is not resilient.

Population resilience can thus be a measure of instability and also a measure of how often we may have to control the pest by chemical means.

In a general way, it is their high resilience that makes insects pests. Small size is coincident with high population growth rates (Southwood 1981). And, within insects, it is also clear why some groups are more of a problem than others: aphids, for example, have particularly high population growth rates. But it is not on such intrinsic factors that I wish to concentrate. Rather, I ask: how does trophic structure modify a species' rate of return to equilibrium? In the specific terms of insect outbreaks, this means asking how trophic structure affects the rate at which outbreaks reach unacceptable levels.

A major determinant of resilience appears to be food chain length: the longer the food chain, the less the resilience of the system's constituent species (Pimm and Lawton 1977, Pimm 1979b, 1982). Thus, removing trophic levels will mean that pest outbreaks will occur faster (Pimm 1984a).

A way to evaluate this idea may also give some insight into why insecticide applications often induce outbreaks. The application of insecticides clearly kills many pests; but many predators are often killed as well. The predators, moreover, require the pests to come back before they can recover. This suggests that there will be a 'time window' following insecticide application, where pests have very few predators and so, according to the theory, should be increasing faster. I pose this question: At comparable densities, do pests increase faster following insecticide applications than in untreated controls?

I might add, parenthetically, that it has often been documented that insect pests can reach higher densities following spraying but this does not necessarily mean they are increasing faster at any particular density. Although this idea seems reasonable, it has not been explicitly tested experimentally. The tests I shall now present are new ones and must be explained in somewhat more detail than those elsewhere in this section.

(b) Methods

(i) Data collection

I restricted my attention to phytophagous aphids and mites on the above-ground parts of cereal, vegetable and orchard crops. I must assume that the population changes observed following insecticidal applications are to a large extent a reflection of reproduction at that time and not due to such processes as soil-emergence and immigration. Many arthropod pests of agricultural crops overwinter as immatures in the soil, before emerging in the spring. If I included species in which soil-emergence is an important cause of within-season increases in numbers, environmental conditions during the previous season would then clearly influence my estimates of the rate of increase of populations. Immigration also can be a dominant force in causing the increases in numbers I observe. Since aphids can be winged in certain life-stages, ideally I should only include counts of the wingless stages. Unfortunately this would severely reduce my data set because most studies did not distinguish the different stages.

Considering these caveats I chose aphids and mites. While I cannot exclude emergence and immigration, the high reproductive capacity of these species, plus other features of their natural history, mean that the changes in numbers I observe will more likely reflect the contribution of population growth.

I included studies on commercially farmed land as well as those using experimental plots. I grouped chemicals according to whether they were (a), applied as granules or liquids into the soil and then covered ("soil applied" pesticides) or (b), whether they were applied as sprays, dusts, or foliage granules above ground ("above-ground" pesticides). It was assumed that pesticides in both categories would reduce densities of herbivorous species while those in the second category only would also severely affect predatory species. Systemic pesticides applied above-ground were considered to be in the second category.

The data I assembled were counts of individual species, groups of species, or of all mites or aphids encountered. Samples involved

one or more life stages. I extracted data from papers appearing in the Journal of Economic Entomology during the years 1957 to 1976. Some papers presented more than one set of data, for example, when more than one pest species, area, or year were studied. All data sets included counts in one untreated plot or field but most sets contained separate measurements from more than one treated plot or field, each receiving a particular amount or type of chemical. In total, I made 112 comparisons between treated and untreated populations from 34 data sets and from 23 papers. From each data set I extracted pest densities on different dates for the control and for each treatment type. The recorded times represented the time-period, in days, between the sampling date and the last treatment date.

I treated the data according to a number of rules which satisfy three general requirements. First, population growth rates should be calculated from density-measurements which are based on samples taken over similar dates for the control and for the treated plots. Second, in order to make valid comparisons between control

and treated populations, I restricted my attention to treated populations which eventually recovered to densities similar to those of the corresponding control populations. Specifically, densities in treated plots had to reach the same order of magnitude as the maximum density-measurement taken from the control plots as a requirement for inclusion. My third requirement was to ensure that only populations that were genuinely increasing were included. I excluded data involved in the drops in populations which often occurred at the end of the season. Details of the data I used for the analysis can be found in Table 1 of Redfearn and Pimm (1987).

(ii) Data analysis

I used two methods.

1) I assumed exponential population growth and applied the following simple linear regression model:

$$\log_{10}\text{density} = a + b\ (\text{time}) \qquad (1)$$

where a is the intercept and b an estimate of 'r', the instrinsic rate of increase in a population.

2) If population growth is not simply exponential i.e. log density does not increase linearly with time, then the addition of a quadratic term to Eq. (1) may improve the model. Therefore, I tested the following model:

$$\log_{10}\text{density} = a + b\ (\text{time}) + c\ (\text{time})^2 \qquad (2)$$

where a, b and c are constants.

Populations may behave in this fashion if, for example, competition for resources were restricting population growth at high densities. (In this case the constant c would be negative.) This case must be considered because any effect of insecticides on population growth rates that I detect from the simple linear model (Equ. 1) may simply be due to comparing population growth rates for the treated and untreated populations at different population densities. The quadratic model (Equ. 2) takes density dependent growth into account and will allow me to compare population growth rates at the same densities for the treated and untreated populations.

(c) Results

(i) Simple linear regression model

Estimates of the rate of population growth

obtained by applying the simple linear regression model are given in Table 2 of Redfearn and Pimm (1987). Values of 'r' are directly related to the amount of time taken for the population to double in density. The units of density used, therefore, do not alter the estimate of 'r'. Units of time, however, are not arbitrary and I have used days as the unit, throughout.

From 60 comparisons, 88% of populations treated with above-ground pesticides had higher r-values than the corresponding control population. The different comparisons from a particular study may not have been independent and so treatments were grouped according to the control with which they were compared. A one-tailed paired t-test on the differences between the means for the treated populations in each such group and the corresponding control population was used. This test showed that, on average, the treated populations increased significantly faster than the controls ($0.0005 < P < 0.005$) (see Table 1).

For populations treated with soil-applied pesticides, only 67% of 52 comparisons had

Table 1. Summary of the results a), assuming exponential population growth and b), if one includes a quadratic term in the population growth model.

	SOIL-APPLIED PESTICIDES			ABOVEGROUND-APPLIED PESTICIDES		
	Overall	Aphids	Mites	Overall	Aphids	Mites
a) Log density = a + b (time)						
Frequency of times r is higher in treated populations than it is in the corresponding control population.	$\frac{35}{52}$ = 67.31%	$\frac{31}{37}$ = 83.78%	$\frac{4}{15}$ = 26.67%	$\frac{53}{60}$ = 88.33%	$\frac{44}{46}$ = 95.65%	$\frac{9}{14}$ = 64.29%
t_r (from paired t-test on control and treated populations' r-values).	0.111	1.173	-1.924	2.893	3.027	0.672
	P>0.4 (df=13)	P>0.1 (df=8)	P>0.05 (df=4)	0.0005<P<0.005 (df=23)	0.0005<P<0.005 (df=14)	P>0.25 (df=8)
b) Log density = a + b (time) + c(time)^2						
Frequency of times r_{inst} is higher in treated populations than it is in the corresponding control populations.	$\frac{21}{51}$ = 41.18%	$\frac{16}{36}$ = 44.44%	$\frac{5}{15}$ = 33.33%	$\frac{45}{55}$ = 81.82%	$\frac{41}{45}$ = 91.11%	$\frac{4}{10}$ = 40.00%
$t_{r_{inst}}$ (from paired t-test on control and treated populations' r_{inst} values).	-0.104	-0.056	-0.085	2.369	3.135	-0.894
	P>0.4 (df=13)	P>0.45 (df=8)	P>0.45 (df=4)	0.025<P<0.01 (df=20)	0.0005<P<0.005 (df=13)	P>0.2 (df=6)

greater r-values than the corresponding control. The t-test showed that these treated populations were not increasing at significantly higher rates than the controls ($P > 0.4$) (see Table 1).

It can be seen from Table 1 that when aphids and mites were analyzed separately, the above situation only held for aphids. For mites, the rates of increase of control populations were not significantly different to those for populations treated with above-ground or soil applied pesticides.

(ii) Model with a quadratic term

There was evidence that at least some of the populations studied were not increasing exponentially; an additional term in $(time)^2$ made, in some cases, a significant improvement on the model. For many populations, however, I could not judge whether the quadratic model was a statistical improvement because I had insufficient density measurements.

For populations receiving soil-applied pesticides, 12 out of the 43 studies in which I had sufficient data, had population growths better modelled by the quadratic equation

(Eq.(2)). This was true for eight control populations out of 16 and one above-ground treated population out of 17. In all cases where the quadratic model was a good fit, the coefficient in $(time)^2$, c, was negative. This result shows that at least some of the populations were increasing progressively more slowly at higher densities.

The non-linear growth raises the following possibility: the application of above-ground pesticides may not have affected population growth rates directly. My previous estimates of 'r' for treated populations may have been higher than those for controls due to sampling at different points along a common curve of log density against time; namely, at lower densities. As we might expect, the density-measurements used to estimate r-values for treated populations were lower, on average, than those for the corresponding control. The lowest density-measurement used for a given treated population was lower than that used for the control in over 75% of the 112 comparisons made in my study.

(iii) Dealing with the implications of non-exponential growth

To test whether my results are altered if one assumes that growth is non- exponential, one would need to compare growth rates of treated and untreated populations at equal densities. I compared instantaneous rates of increase (which I call r_{inst}) at a density (y^*) midway between the mean log densities of each corresponding treated and control population. This procedure was carried out for all data sets. The equation,

$$T^* = \frac{-b + (b^2 - 4(a - y^*)c)^{1/2}}{2c} \qquad (3)$$

gives the time (T^*) when the density y^* occurred in each treated and control population. The parameters a, b, and c were obtained from the quadratic statistical model (Eq. (2)). Instantaneous population growth rates can then be found by substituting the result from Eq. (3) into :

$$r_{inst} = b + 2c(T^*) \qquad (4)$$

The estimate of r_{inst} for each treated population was thus compared with a unique estimate for the corresponding control at the

same density, y^*.

The estimates of r_{inst} from this analysis are included in Table 2 of Redfearn and Pimm (1987). In 6 cases (left as blanks in the table), Eq. (3) could not be solved and r_{inst} could not be calculated. From 55 comparisons, however, 82% of populations treated with above-ground pesticides had higher instantaneous r-values than the corresponding control. A one-tailed paired t-test compared the mean instantaneous r-values obtained for treated populations averaged over each data set, with the mean values for the controls. The test showed that the treated populations had significantly higher instantaneous r-values than the controls ($0.025 < P < 0.01$) (see Table 1).

For populations treated with soil-applied pesticides, only 41% of 51 comparisons had greater instantaneous r-values than the control. The t-test showed that there was no significant difference between control and treated populations in this respect ($P > 0.4$) (see Table 1). These results parallel those from the exponential model. Again, when mite populations

were analyzed separately, their instantaneous r-values were not significantly increased by either category of pesticide (see Table 1).

(d) Summary

Use of above-ground pesticides causes accelerated population growth in aphids but not in mites. This accelerated growth is not due entirely to the fact that these insecticides might release the aphid populations from some density-dependent factor, such as resource-limitation which affects the untreated populations at high densities. I reach this conclusion because my results were not altered by assuming density-dependent growth and comparing estimates of the instantaneous rates of increase of treated and untreated populations at equal densities. Furthermore, it is unlikely that the accelerated growth caused by above-ground pesticides was entirely a consequence of the removal of herbivorous species competing with the aphids. These will have been attacked by soil-applied pesticides, which had no significant effect on the population growth rates of the aphids.

One hypothesis is consistent with the fact that above-ground insecticides cause increased population growth rates in aphids. These insecticides not only destroy pests, they also severely reduce predator densities. Predators, moreover, require their prey to recover before they themselves can return. Thus, immediately following treatments with these insecticides the pests have few predators, food chains are effectively shortened, and population growth rates are increased. The fact that soil-applied insecticides had no effect on population growth rates is consistent with these ideas. These insecticides are expected to have less of a deleterious effect on predators than above-gound insecticides have.

A more detailed study is required to determine why these results apply to aphids but not mites. Aphids and mites may suffer from different degrees of predation and their capacities for increase - either through reproduction or by colonization - are likely to differ.

4. VARIABILITY

(a) Introduction

Since Elton (1958) clearly equated variability with instability, a number of studies have examined how variable are insect populations. Variability, on a year-to-year basis, is not difficult to calculate. Rather more difficult are attempts to understand and predict what the trends in variability should be. How much a population varies may depend on the trophic structure of the community to which a species belongs. But it is also likely to depend on the variability of such extrinsic factors as the weather. Moreover, there is a general tendency in biological data for variability to increase with the mean, although such measures as the coefficient of variation (standard deviation/mean) may avoid such a trend. Simply, variability might be among the more difficult kinds of 'stability' in which to detect trends.

(b) Two alternatives

We might expect a close tie between variability and resilience. Resilient populations return quickly to equilibrium and

thus may be expected to stay closer to that equilibrium and vary less than populations that are not resilient. But Turelli (1978, 1986) has pointed out that this is not the only argument that can be made. In fact, there is an argument that leads to a diametrically opposite result. Resilient populations may chase continually fluctuating resources, while less resilient ones may average out such variations. For bird (Pimm 1984b) and fish (May et al. 1978) populations, the first argument seems to be the better description of nature: more resilient populations vary less. For noctuid moths, Spitzer et al. (1984) have shown the opposite: species with the greatest fecundity and potential rates of increase were the most variable.

(c) Empirical studies

Looking at variability directly has produced some interesting studies. Wolda (1978) has evaluated Elton's (1958) contention that tropical populations vary less than temperate ones. By comparing a large number of population studies, Wolda showed that this was not the case. But populations did appear to be more variable in

systems, such as deserts, which we might expect to have a less predictable climate.

Watt's (1965) study is more closely related to trophic structure. He analysed data collected by the Canadian Forest Insect Survey (McGugan 1958, Prentice 1962, 1963) on 552 species of forest Macrolepidoptera. He used this data set to answer two questions. 1) How does the number of host plant species utilized affect population variability? 2) How does the number of species of competitors affect population variability?

i) Variability and the number of host plant species

Watt (1965) first separated gregarious larval feeders from solitary larval feeders since he had already observed that the former were generally more abundant and more variable. For both of these broad categories, he grouped species of Macrolepidoptera according to their number of tree host species. He then calculated the standard error of the logarithms of the yearly counts for each species and found the mean of this measure of variability for each group. He concluded that groups of moths that had many

host trees were generally more variable than specialized groups. This result was obtained by combining data from all regions of Canada.

Watt (1965) suggested the amount of 'available habitat' was the central feature in determining variability. Thus, trophically generalized species would have more available habitat than specialized ones, and would be able to reach higher numbers during periods of favorable conditions. Watt went on to note the spruce budworm, Choristoneura fumiferana (Clemens), as a species which, though trophically specialized, is highly variable but which occurs over large areas of almost pure stands of its food supply (and available habitat).

I have performed a similar analysis for aphid counts from suction traps located at Silwood Park, England. Counts for the years 1969 to 1983 were obtained from the Rothamsted Experimental Station Reports (Taylor and French 1970-1981, Taylor et al. 1982-1984). I calculated the standard deviation of the logarithms of the yearly counts of 28 aphid species. I found the total number of British

plant genera fed upon by each species from Tatchell et al. (1983). I found that the measure of variability was significantly negatively correlated with the number of host plant genera ($F = 4.25$; $P = 0.0495$). Highly polyphagous aphid species were less variable, on a year to year basis, than specialized species (see Fig. 3).

The results of the two analyses (Watt's, mine) are apparently contradictory and both data sets need further attention before any definite explanations can be presented. However, one difference between the two analyses stands out. Watt studied Macrolepidoptera inhabiting perennial forests in Canada, while I examined aphids living in far more ephemeral, disturbed habitats, namely agroecosystems. Herbivorous insects living in undisturbed habitats may be more effectively controlled by predators than those of disturbed habitats. Risch et al. (1983) discuss the arguments for the view that control by predators may be more important for herbivores on perenniel plants than for those on annual plants. Thus, perhaps Watt's more polyphagous species were more variable because they were able

Figure 3. Standard deviation of the logarithms of yearly counts of different aphid species at Silwood Park, England versus the number of host plant genera for each of those species. The aphid species are: 1-Acyrthosiphon pisum (Harris), 2-Amphorophora rubi (Kaltenbach), 3-Aphis fabae Scopoli, 4-Aulacorthum solani (Kaltenbach), 5-Brachycaudus helichrysi (Kaltenbach), 6-Brevicoryne brassicae (Linnaeus), 7-Cavariella aegopodii (Scopoli), 8-Drepanosiphum platanoidis Schrank), 9-Dysaphis plantaginae (Passerini), 10-Elatobium abietinum (Walker), 11-Eriosoma ulmi (Linnaeus), 12-Hyalopterus pruni (Geoffroy), 13-Hyperomyzus lactucae (Linnaeus), 14-Macrosiphum euphorbiae (Thomas), 15-Megoura viciae Buckton, 16-Metopolophium dirhodum (Walker), 17-Metopolophium festucae (Theobald), 18-Myzus ascalonicus Doncaster, 19-Myzus certus (Walker) and Myzus persicae (Sulzer), 20-Myzus ornatus Laing, 21-Nasonovia ribisnigri (Mosley), 22-Phorodon humuli (Schrank), 23-Phyllaphis fagi (Linnaeus), 24-Rhopalosiphum insertum (Walker), 25-Rhopalosiphum maidis (Fitch), 26-Rhopalosiphum padi (Linnaeus), 27-Sitobion avenae (Fabricius), 28-Sitobion fragariae (Walker).

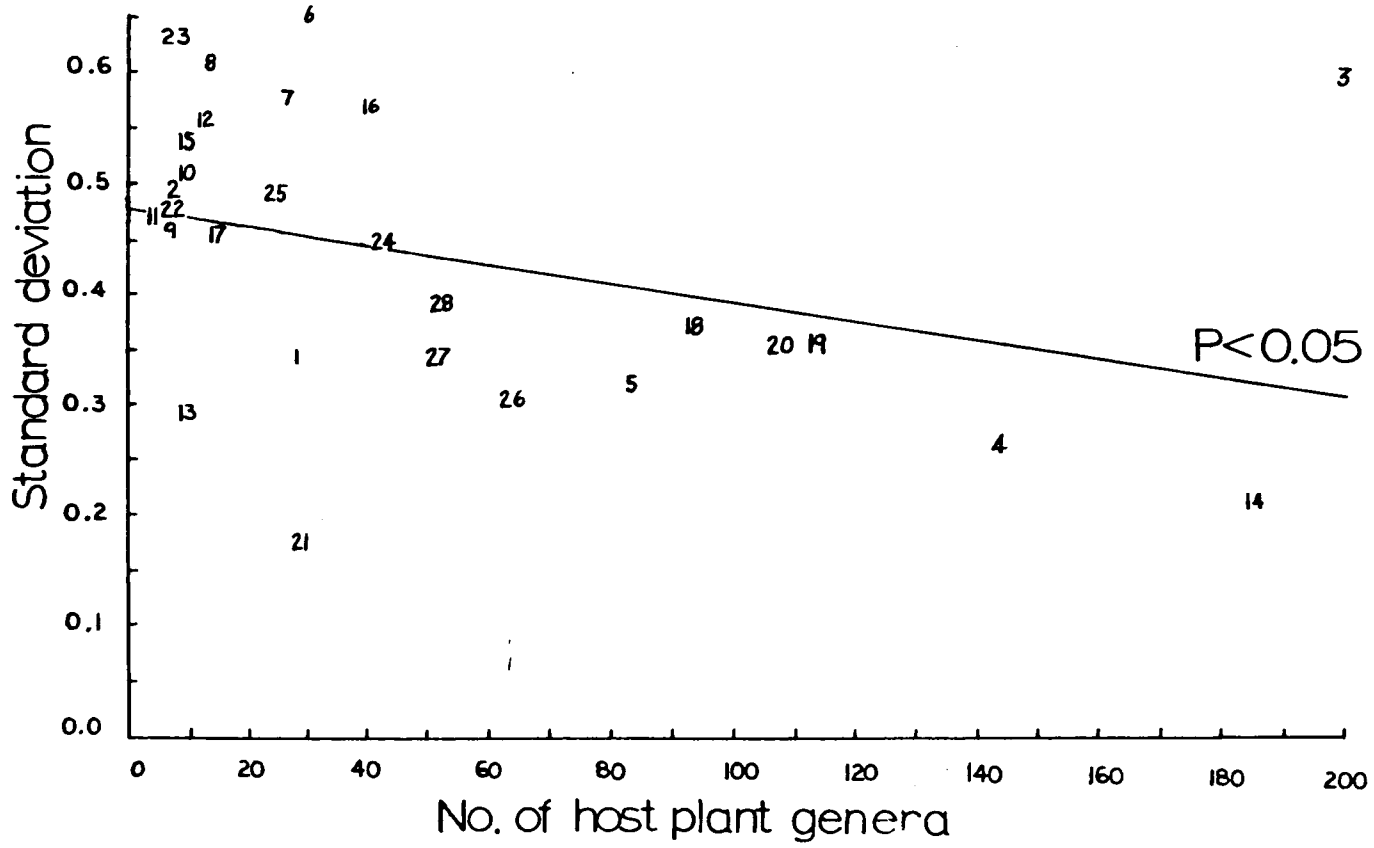
Standard deviation
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
20
40
60
80
100
120
140
160
180
200
No. of host plant genera
P<0.05
23
6
8
3
7
16
12
15
10
2
25
22
11
9
17
24
28
18
20
19
1
27
5
26
13
4
14
21

Figure 3.

to reach high numbers during those few times when predator densities were low. In contrast, changes in aphid population densities in British agroecosystems may largely reflect changes in resource availability rather than changes in predators. Polyphagous aphids have a greater choice of alternative food plant species and so may be less susceptible to the loss of one species, (and thus be less variable) than specialized species, which may fall to lower population densities during unfavorable years. This is essentially MacArthur's (1955) argument, that I discussed earlier.

ii) Variability and the number of competing species

Watt (1965) also used the Canadian Forest Insect Survey data to show that species of Macrolepidoptera which shared host plant species with many other insect species were, on average, less variable than those Macrolepidoptera species which had few potential competitors. This result is perplexing and 'potential' is the key word: Strong et al. (1984) and Lawton and Strong (1981) make a persuasive case that competition for

resources is not a pervasive feature of herbivorous insect communities. They do show, however, that the number of insect species per plant species is closely correlated with the size of the plant species' geographical range -- particularly for plant species with similar physical structure. (Watt's data are all for trees.) Thus, herbivorous insect species feeding on widely distributed plant species are expected to compete with more species than insects feeding on plants with a narrow geographic range. This would seem to translate Watt's second result into: 'populations of insects on more widely distributed plants are less likely to be variable; a result which is not immediately reconcilable with his idea that species with more available habitat are more variable.

5. SUMMARY AND DISCUSSION

To develop my ideas I have noted several definitions of stability, of which three seem particularly relevant to studies of insect pests. 1) Stability in the strict sense of a population returning (or not, if unstable) to some

equilibrium value. 2) Resilience, which measures how fast a population recovers to some equilibrium level following a disturbance. In the case of pest species, that equilibrium may be at a very high density that is unacceptable to man. 3) Variability. A highly variable population will sporadically reach unacceptable levels.

The relationships between trophic structure and these kinds of instability are varied. Despite early suggestions, there seems to be nothing inherently unstable about simple communities. Theory predicts that communities should be simple, relative to what they could be (Fig. 1a), and data show this to be the case. (Fig. 1b.) There are some natural stable communities whose floristic simplicity approaches that of agricultural monocultures. Simply, pest outbreaks in agricultural systems do not appear to be an ecologically inevitable consequence of trophic simplicity.

The actual process of simplifying a trophic structure will almost certainly cause changes in the densities of the remaining species. But it

is far from obvious how and if plant removals will predispose the remaining herbivores to become pests. Actual studies which compare herbivores in monocultures with those in multi-species plantings show that many species do increase in density in monocultures. Detailed studies, however, refute the idea that this is related to changes in the control effected by the predators.

Populations do appear to be more resilient, the simpler the system's trophic structure.

Temperate population densities seem no more variable than tropical ones. The relationship between variability and the degree of polyphagy can be either negative or positive. It is possible that in predator-limited groups, polyphagous species can attain unusually high densities when their predators are unusually rare. Monophagous species will not reach such high densities and will thus vary less. For resource-limited groups, polyphagous species may vary less than monophagous species, because the polyphages are less susceptible to the failure of one of their food plant species.

I have presented the thesis that insect pest outbreaks may be considered as 'dynamic instabilities' and instability may be related not just to the intrinsic properties of the species, but to the trophic structure of the community to which the species belongs. Though the results are varied, the thesis seems correct and it argues persuasively for our recognizing the trophic structure of the community in which an outbreak occurs.

III. POPULATION VARIABILITY AND POLYPHAGY IN HERBIVOROUS INSECT COMMUNITIES

1. INTRODUCTION

Ecologists use the word 'stability' loosely; consequently the term has come to mean many different things (Pimm 1984a). One of its earliest meanings (e.g. in Elton 1958) is low variability in density over time. Three kinds of factors affect density fluctuations. First, different environments may differ in the variability of abiotic variables that determine the abundance of critical resources (Pianka 1986, Wolda 1978). Second, populations of different species have different intrinsic growth rates. A high growth rate may reduce or increase variability (May et al. 1978, Turelli 1978, 1986). Third, we would expect the trophic structure of the community in which a population is embedded to be of crucial importance. One important aspect of community structure is the diet breadth, or degree of polyphagy of an individual population. How does the degree of polyphagy affect insect population variability?

I begin answering this question by reviewing comparative studies of population variability and polyphagy and examining the hypotheses of these studies. Early studies (Watt 1964, 1965, 1973, Rejmanek and Spitzer 1982) have suggested a positive correlation between population variability and the degree of polyphagy. Next, I assemble data from three studies of herbivorous insects and show that the correlation, if it exists, appears to be negative. Polyphagous species have a tendency to be less variable than more specialized species. I will conclude with a brief discussion of the implications of our results.

(a) The Approaches

While ecologists frequently examine the causes of population fluctuations, relatively few studies have addressed the question of what determines the magnitude of this variation. Such studies must inevitably compare populations.

My approach is to consider all interactions (predatory, competitive etc.) of a given species, find that species' variability, and compare with other species. This is Watt's

(1964, 1965, 1973) method. In this way, we can look at the effects of each type of interaction separately before examining the combined effects of all types. For herbivorous insects, we can look at the effects on a species' population variability of the number of its potential competitors, the number of host plants on which it feeds, and the number of predator and parasite species that attack it.

Competitive interactions are difficult to discern and, in any case, there is a widely held view that competition for resources is not an important process structuring herbivorous insect communities (Strong et al. 1984, Lawton and Strong 1981). I am currently assembling data on predators and parasites and will present the analyses elsewhere. Here I ask: in herbivorous insects, are populations of polyphagous species more, or less, variable through time than those of more host-specific species?

(b) Theoretical arguments

MacArthur (1955) argued that species with many food species should be less susceptible to population reductions and so should be less

variable than more specialized species. If one host-type of a polyphagous species becomes unavailable or rare, then individuals could switch to alternative food types. Host-switching is not necessarily required for this argument, however. Fox and Morrow (1981) point out that some polyphagous insect species may be composed of separate sub-populations that each specialize on different local hosts. In the case of such a species, when one type of host becomes unavailable only a relatively small fraction of the species' total population is likely to suffer from poor resource levels: fewer sub-populations will be affected. This might, for example, be important for those aphid species that are composed of a number of different biotypes, each with slightly different host preferences (Eastop 1973).

Watt (1964, 1965, 1973) analyzed data on the immature stages of 552 species of forest Macrolepidoptera collected by the Canadian Forest Insect Survey (McGugan 1958, Prentice 1962, 1963). His results contradict MacArthur's prediction: species with a wide variety of host

tree species were more variable than specialist species. Watt (1964) suggested that this result is best explained in terms of available habitat rather than by host-diversity per se. During rare favorable conditions, polyphagous species should be able to feed in a higher proportion of the total habitat, spend less time searching and, thus, be able to reach high numbers faster than most host-specialists. Watt found that certain specialist species were particularly variable, however. The Spruce Budworm, Choristoneura fumiferana (Clemens), is an example. According to Watt, this is because the Spruce Budworm lives in habitats where its principal hosts, Balsam Fir, Abies balsamea (L.) Mill., and White Spruce, Picea glauca (Moench.) Voss., occur in stands with few other tree species to impede the budworm's host-finding efficiency. Thus, Watt argued that, even though polyphagous species were generally more variable, certain specialist species' populations may fluctuate strongly, since they may, on occasion, attain extremely high densities where their hosts are the dominant species. This sort

of phenomenon is also explained by Root's (1973) resource concentration hypothesis: non-host plants may mask a herbivore's host-finding cues and reduce the likelihood of outbreaks.

Rejmanek and Spitzer (1982) also found a positive correlation between measures of population variability and the degree of polyphagy for Noctuid moths in South Bohemia.

The two opposing arguments are summarized by Fig. 4. The figure is a deliberate over-simplification, intended only to summarize the essential points: MacArthur's hypothesis relates to the effects on deviations below a norm ("crashes"), while Watt's argument explains deviations above ("outbreaks"). Two comments are relevant here. 1) The two hypotheses are not mutually exclusive. While variability is a consequence of both unusually low and unusually high numbers, the relative importance of either in determining overall variability may depend on the particular system under study. 2) Many authors (Elton 1958 and Pimentel 1961, for example) equate rarity of outbreaks with stability. Outbreak frequency is clearly

Figure 4. Caricature of the two opposing arguments of MacArthur (1955) and Watt (1964). MacArthur suggested that specialist species may be more variable because they are likely to be more succeptible to population crashes. Watt said that polyphagous species may be more variable because they may be able to attain higher numbers during favourable periods.

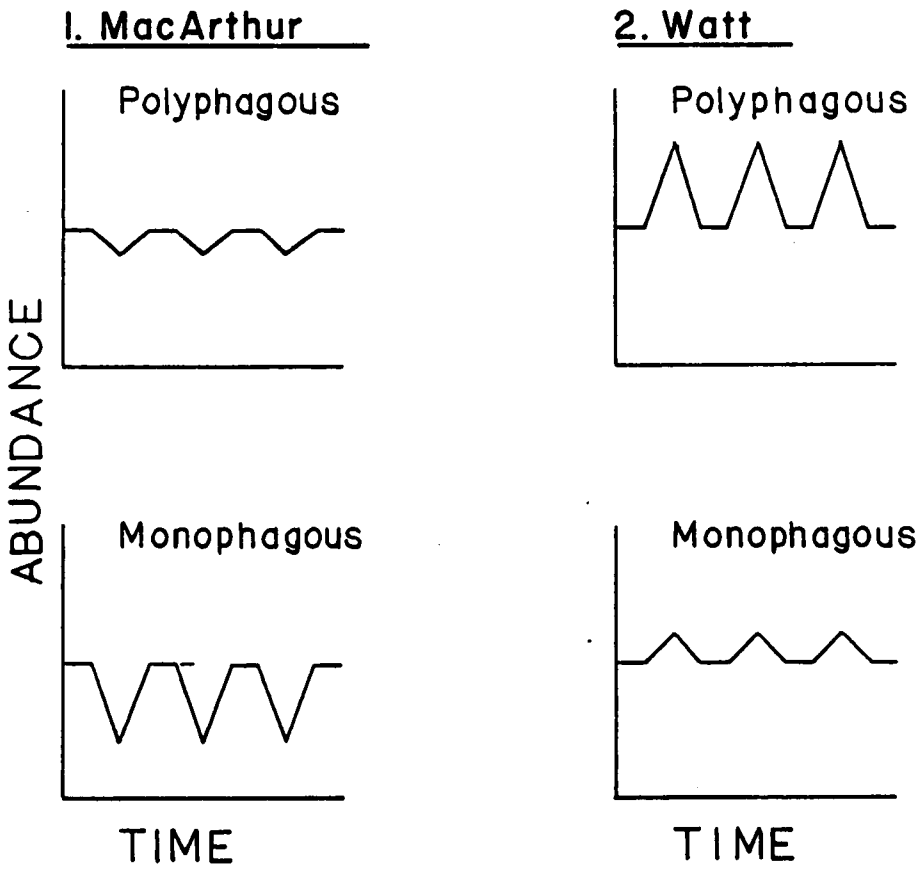
1. MacArthur
2. Watt
Polyphagous
Polyphagous
ABUNDANCE
Monophagous
Monophagous
TIME
TIME

Figure 4.

important in agriculture: it may determine how often pesticide applications are required. How often crashes occur may be of less interest. MacArthur's argument, in contrast, emphasizes that frequency and severity of crashes also need to be considered when estimating total population variability.

2. METHODS

Here I examine the relationship, if any, between population variability and the degree of polyphagy in two groups of insects and in two regions. I look at British aphids, British moths and re-evaluate the Canadian Macrolepidoptera studied by Watt. A preliminary analysis involving British aphids presented in Redfearn and Pimm (1987) suggested the opposite result to that from Watt's (1964, 1965, 1973) study: polyphagous British aphid species tended to be less variable than monophagous ones. My initial reason for re-examining Canadian Macrolepidoptera was to attempt to understand that difference.

In compiling data that were collected for purposes other than my own, I must make a large

number of decisions about what to include and exclude and how the data are to be treated. This 'Methods' section is inevitably long and detailed. In the first part of this section, I indicate that I am using estimates of variabilities and abundances based on logarithmically transformed data. In the second part, I present the details of how I selected data from the original sources to meet my requirements. The reader can omit this part without a loss of continuity. In the final part, I outline the problems of detecting an effect of polyphagy on variability, in the face of various confounding relationships. In particular, population abundance may be expected to correlate with polyphagy and its effects must be factored out. How I do this also requires many details and this section may also be skipped without loss of continuity.

(a) Data Analysis

For all three data sets, my measure of a species' population variability was the standard deviation (SD) of the logarithmically

transformed yearly abundances. Thus, for a given species,

Variability = SD [$\log_{10}$(yearly abundance + 1)]

I used the log transformation because changes in population densities are multiplicative rather than additive. Therefore, a logarithmic rather than arithmetic scale tends to normalize the population densities (Taylor and Woiwod 1980, Williams 1937, Williamson 1972, 1984). I added 'one' to the abundances so that the log transformation did not exclude zero years from the population record (Taylor 1986). For a measure of mean abundance I used the mean, over all years, of the logarithmically transformed yearly abundance.

These two estimates were only calculated for a species if there were at least 10 years during which at least one individual was collected per year. Thus, species that were infrequently caught by the various methods were not analyzed, since population measures for such species may not be reliable. Because of this precaution, less than 2.5% of the observations included were zeros. In the case of British aphids and moths,

fewer than 7% of the species in the original data set were removed. For Canadian Macrolepidoptera, however, the precaution meant that two-thirds of the original species were excluded from my analysis.

(b) Data sets analyzed

(i) British aphids

I analyzed data collected by the Rothamsted Insect Survey in the years 1970 to 1983, appearing in the Rothamsted Experimental Station Reports (Taylor and French 1971-1981, Taylor et al. 1982-1984). These are monthly counts of alate aphids of economic importance collected in suction traps at a height of 12.2 meters. The traps are located in agricultural land.

I ignored records from 1969 and earlier because of trap operation problems, which were solved in 1970 (Taylor and French 1970, 1971). I summed the monthly counts in order to obtain yearly totals. For a given species and a given year the totals represent abundances relative to other years and so the data are appropriate for studies on variability. We cannot expect, however, that these totals are accurate measures

of the actual abundances of the species, since some species may be more readily caught than others.

During most years the trap records are from 26 March until 4 November. For two years, however the records were not started until 23 April. For consistency, my yearly totals always represent the sums of counts from 23 April until 4 November.

I confined my attention to just six of the many collection sites located around Britain (see Appendix I of Redfearn and Pimm 1988). These six were picked to represent a range of north-south locations. I estimated population variability and mean abundance at each individual site separately.

The Rothamsted annual reports give records of over 30 species. I ignored some species because of a lack of information about plant hosts. The variabilities of some species were not calculated because I felt that the abundance records were not reliable. For example, Myzus persicae (Sulzer) and M. certus (Walker) were counted as a single species group in the reports

until 1975. Chaetosiphon fragaefolii (Cockerell) was recorded infrequently at all of the sites, and so was also excluded. Rhopalosiphum insertum (Walker) and R. padi (Linnaeus) were included in my analysis but were not reliably distinguished until 1971, so for these species, the 1970 counts were excluded from my estimates of variability.

For periods during certain years and at certain sites, the suction traps ceased to operate. Those years were discarded from my analysis for those sites. This was the case for the year 1981 for Dundee, 1973 and 1978 for Newcastle, and the years 1970, 1978, 1980 and 1981 for Elgin. Appendix I in Redfearn and Pimm (1988) shows the data for each of the six sites. Variability and mean abundance were calculated for a total of 26 species.

For each species analyzed, I obtained a measure of the degree of polyphagy from Tatchell et al. (1983) (see Appendix I of Redfearn and Pimm 1988). This source provides the total number of British plant species on which the aphid species has been recorded. This is a

measure of the potential diversity of hosts used by a species. I do not suppose that all of the plant species act as hosts at all times, in all years, and at all sites.

(ii) British moths

Here again, I analyzed data from the Rothamsted Insect Survey, but from the years 1966 to 1982, as the data appeared in Rothamsted Experimental Station Reports (Johnson 1969, Taylor and French 1970-1981, Taylor et al. 1982-1984). These give yearly counts of various moth species of economic interest collected in light traps at a height of 1.2m, situated in a wide variety of environments. As was the case for aphids, the counts estimate relative year-to-year abundances of the different species (Taylor 1979).

I restricted my attention to a total of 15 sites in Britain (see Appendix II of Redfearn and Pimm 1988). These sites represent a wide range of latitudes.

The reports present data from 31 species of moths; I analyzed the 25 species listed in Appendix II of Redfearn and Pimm 1988. Three

species included in the reports (Plutella maculipennis Curtis, Udea ferrugalis Hubner and Nomophila noctuella Denis & Schiffermuller) were excluded because of a lack of information on host plants, while another three (Euproctis chrysorrhoea Linnaeus, Nycterosea obstipata Fabricius and Laphygma exigua Hubner) were removed because of the infrequency with which they occurred at all the sites.

At many of the sites, only a limited number of species were collected often enough to enable me to calculate population variability. Therefore, I estimated variability (and mean abundance) by summing each year's counts across all the sites; hence, for moths, I am estimating variability over a much larger spatial scale than for aphids.

For some sites there were no records available for any species for one or a few years. For example, there were no records at all from Rowardennan, Scotland for the years 1973-1975. There were also cases where counts for certain species are missing for certain years. For example, at Dundee, there was no

record for Alsophila aescularia Denis & Schiffermuller in 1966. Such gaps in the record cause problems when summing over different sites. One must be sure that, for each species, the same number of sites are represented in the yearly totals in all years, otherwise yearly variability would merely reflect variability in the number of sites included. To overcome this problem, I applied the following procedure for each species: I found the year for which there was the lowest number of sites where there was a record available. The appropriate number of site records were ignored for the other years so that all yearly counts of the species were the sums over the same number of sites. For most species, 12 sites were pooled each year; the minimum was 10 sites (see Appendix II of Redfearn and Pimm 1988). Wherever possible, I pooled the same sites each year for each species.

I know of no source in the literature that gives detailed records of the hosts of British moths. I made a qualitative assessment of the degree of polyphagy of each species based on its description in a field guide by Skinner (1984).

I assigned each species to one of three groups (see Appendix II of Redfearn and Pimm 1988): "relatively specialized", "intermediate" and "relatively polyphagous". For example, Bupalus piniaria Linnaeus, is described as feeding on only two species of pine; it was considered "relatively specialized". In contrast, Plusia gamma Linnaeus was described as feeding on almost all kinds of wild and cultivated low growing plant and was considered "relatively polyphagous". The descriptions of feeding habits given by Skinner (1984) are based on larval stages, while the yearly counts used to estimate variability are of adults. My assumption is that variability in adults is a reflection of events during the larval stages.

(iii) Canadian Macrolepidoptera

Like Watt (1964, 1965, 1973), I analyzed data from the Canadian Forest Insect Survey. The survey was only intended to provide approximate indices of abundance (Watt 1964). The data set is so large, however, that I may be able to make broad conclusions based on statistical analyses of large numbers of species

(Watt 1964).

The three volumes of data analyzed by Watt (McGugan 1958, Prentice 1962, 1963) summarize 614 species from all families of Canadian Macrolepidoptera. The data are yearly counts of immature stages of Macrolepidoptera collected by hand-picking and by beating trees. The yearly totals represent the summed collections from areas in various parts of Canada and, again, they are merely measures of relative abundances.

In my analysis, I followed Watt and excluded pre-1945 data. I calculated variability and abundance of 204 species from 13 families (see Appendix III of Redefearn and Pimm 1988). Many species in the original data set were discarded from my analysis because they were not found during a sufficient number of years.

The original data include the number of different host tree species on which the collected larvae were found feeding. This is the estimate of the degree of polyphagy used by Watt (1964, 1965, 1973). This measure, unfortunately, is strongly dependent on the estimates of abundance. For example, if one uses

this estimate of polyphagy, then a species that was collected 10 times could have, at the most, 10 host tree species. A species collected on 100 occasions could have up to 100 host species. We need an estimate of the degree of polyphagy that is independent of the data used to estimate abundance and variability. Tietz (1972) provides such a source for this estimate in his compilation of the number of plant genera on which the moth species have been recorded. (The source covers the literature through the year 1950 and did not enable me to estimate the number of host species with certainty.) As before, this estimate reflects the potential host diversity of the phytophagous insect species. This measure of polyphagy was found for 151 of the 204 species of Macrolepidoptera analyzed (see Appendix III of Redfearn and Pimm 1988).

(c) Confounding factors

My goal is to find out how the degree of polyphagy affects population variability. There are, unfortunately, factors which may mask the relationship of interest, or may confuse the issue in some other way (Fig. 5).

Figure 5. Possible confounding factors which may mask A), the relationship of interest. 1) Abundance and polyphagy may be related. 2) Abundance and variability may be related. 3) The characteristic lifestyle of the particular species may influence abundance, variability and any of the other three relationships (see section 2(c)(iii)).

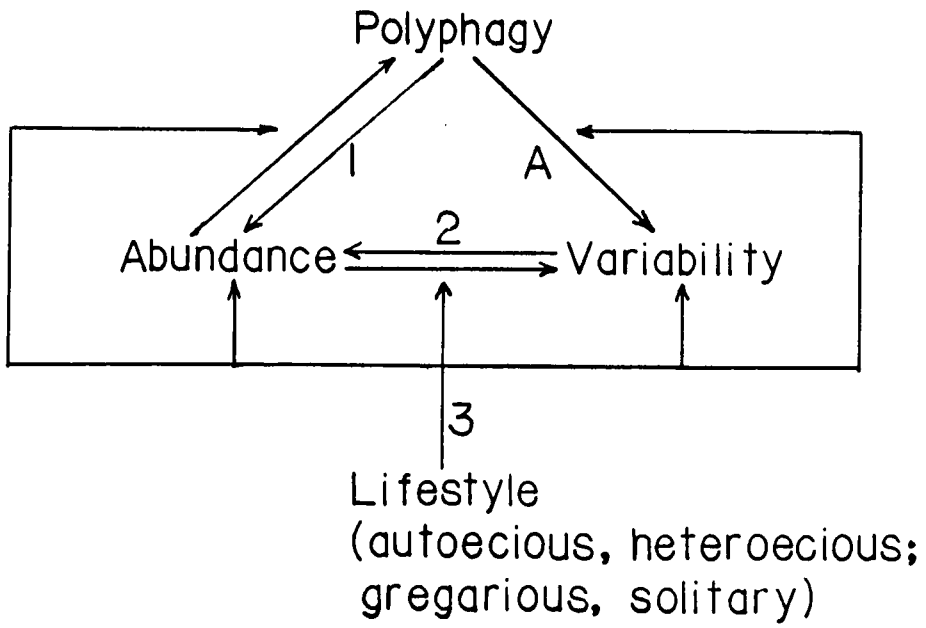
Polyphagy
I
A
2
Abundance
Variability
3
Lifestyle
(autoecious, heteroecious;
gregarious, solitary)

Figure 5

(i) Abundance-polyphagy

A rare species may appear to be more specialized than it really is, simply because of insufficient host records. Conversely, a highly polyphagous species may, in some cases, be more apparent to field biologists than a specialized species. It may be collected more frequently and appear more abundant.

(ii) Abundance-variability

A species that usually has a relatively constant population density, but reaches an abnormally high level in one year, might appear to have a greater variability than a species that fluctuates continually over low densities. Logarithmic transformations of the data remove much of the dependence of variability on the mean abundance (Williamson 1972, Wolda 1983). Nonetheless, there is still the possibility of a relationship between variability and mean abundance in log-transformed data and I should investigate this possibility and discuss its consequence if it arises.

Suppose abundance is correlated with

polyphagy or with variability. Is abundance necessarily then a confounding variable? When I account for the effects of abundance on the variables of interest, am I removing effects that are part of the phenomenon that I am investigating? Certainly, if abundance and polyphagy are related due to sampling error, and if abundance and variability are related because of purely statistical reasons, then of course, I should remove these effects. But, if polyphagous species really are able to reach higher abundances than specialist species, and population fluctuations reflect this (which is the basis of Watt's argument), then abundance is not a confounding variable. The question, therefore, is: should I, or should I not, remove the effects of abundance? There is no easy answer, since a correlation analysis does notgive the direction of causation. My approach is to analyse the data both ways, i.e., 1) by viewing any correlations between abundance and polyphagy (or variability) as artifacts and so correcting the estimate of polyphagy (or of

variability) and 2) by viewing the uncorrected estimates as being the interesting ones.

(iii) The characteristic lifestyle of a particular species

The lifestyle of a species may affect its abundance or its variability. Furthermore, lifestyle may influence any of the possible relationships discussed above. Watt (1965), for example, found that in Canadian forest Macrolepidoptera, gregarious larval feeders were generally more abundant and variable than solitary species. He also suggested that there was a stronger relationship between variability and polyphagy in solitary species than in gregarious species. The lifestyles of the Canadian Macrolepidopteran species that I analyzed were determined from McGugan (1958) and from Prentice (1962, 1963). Of the 204 species analyzed, only 16 were gregarious larval feeders (see Appendix III of Redfearn and Pimm 1988).

In aphids, a relevant dichotomy may be between heteroecious ("alternating") species and autoecious ("non-alternating") species (Blackman and Eastop 1984, Dixon 1984, Tatchell

et al. 1983). Heteroecious species spend autumn, winter and spring on some "primary", usually woody host, on which they may lay eggs, but spend the summer on "secondary" hosts from different families to the primary hosts. The secondary hosts are usually herbaceous. Autoecious species show no such alternating preferences for hosts. The lifestyle (alternating or non-alternating) of each aphid species was determined from descriptions in Tatchell et al. (1983) and Blackman and Eastop (1984) (see Appendix I of Redfearn and Pimm 1988). The situation was not clear-cut in all cases, such as in Cavariella aegopodii (Scopoli), which alternates in only part of its range. In such cases, the species was assigned to its most generally used lifestyle in Britain, according to Tatchell et. al. (1983). Preliminary analyses suggested that alternating species were, on average, more abundant and slightly less variable at certain sites than non-alternating species.

3. RESULTS

(a) British aphids

As already noted, abundance may correlate with variability (even when we logarithmically transform the data) and with polyphagy scores. Thus, I start each part of this section with a determination of whether I should correct the estimates of variability and polyphagy for abundance.

There was no relationship between mean log abundance and standard deviation for any group of aphids at any of the six sites.

I found a slight, but possibly confounding, positive relationship between mean log abundance and the degree of polyphagy ($P=0.08$). For this test, I used a measure of overall mean log abundance in Britain, taken directly from the appendix in Taylor and Woiwod (1980). Appendix I of Redfearn and Pimm (1988) shows the overall mean log abundances of all species involved in the test.

I attempted to factor out the effects of

abundance on polyphagy by using the residuals about the regression line as a corrected measure of polyphagy. Unfortunately, these residuals were skewed: the great majority were negative. The residuals about the relationship between the logarithmically transformed measure of polyphagy and mean log abundance ($P=0.01$) were not so highly skewed, so I have used these residuals as the corrected measures of polyphagy (see Appendix I of Redfearn and Pimm 1988). I regressed the corrected estimate of polyphagy against the uncorrected measure of variability, treating the two lifestyles (alternating, non-alternating) seperately in an analysis of covariance. Table 2 gives the results of the analysis for each of the six separate sites. In non-alternating species, polyphagous species tended to be less variable than more specialised species. There was a negative relationship for all six sites and for three of the sites (Dundee, Newcastle and Silwood Park) this relationship was significant in a two-tailed test.

In alternating aphid species, I found no

Table 2. Analysis of covariance of variability versus polyphagy (corrected for abundance) for the two life-styles of British aphid species (A=alternating, NA=non-alternating). (Polyphagy was corrected for abundance by taking the residuals about the regression line for the relationship between measures of polyphagy and abundance - see text.) In model A), the two lifestyles were not assumed to have parallel regression slopes. I give the slope of the regression line, the probability (P) that the slope is zero (the number of species involved in the test are given in parentheses), and the probability that the two life-styles have the same slopes. In model B), the two life-styles are assumed to have parallel regression slopes. I give that slope, and the probability that it is zero.

	(A) DIFFERENT SLOPES MODEL			(B) SAME SLOPES MODEL	
SITE	SLOPE	P	SLOPES THE SAME?	SLOPE	P
Elgin NA	-0.2269	0.1394(7)	P=0.4754	-0.1521	0.1534
Elgin A	-0.0763	0.6088(11)			
Dundee NA	-0.2543	0.0126(11)	P=0.0775	-0.1448	0.0697
Dundee A	0.0167	0.8833(12)			
Newcastle NA	-0.1800	0.0335(10)	P=0.0412	-0.0715	0.2978
Newcastle A	0.0919	0.3476(10)			
High Mowthorpe NA	-0.0480	0.6784(10)	P=0.2286	0.0506	0.5503
High Mowthorpe A	0.1566	0.2016(12)			

Table 2 (continued)

SITE	(A) DIFFERENT SLOPES MODEL			(B) SAME SLOPES MODEL	
	SLOPE	P	SLOPES THE SAME?	SLOPE	P
Silwood Park	NA -0.2330	0.0073(12)	P=0.2737	-0.1757	0.0077
	A -0.0974	0.3000(13)			
Wye	NA -0.0952	0.1979(12)	P=0.6531	-0.0740	0.1800
	A -0.0450	0.5969(13)			

clear relationships between polyphagy and variability. Three of the sites (Elgin, Silwood Park and Wye) exhibited negative regression slopes, the rest showed positive slopes. At no site was there a significant relationship.

At all sites, the regression slope for non-alternating species was more negative than that for alternating species. This difference was significant for Newcastle and marginally so for Dundee.

Fig. 6 is a graph of the data for Silwood Park. The apparently outlying alternating species in the top right-hand corner is Aphis fabae Scopoli. Silwood Park is typical in this respect. In order to examine whether the apparent difference between the alternating and non-alternating species was merely due to A. fabae, the above analysis was repeated, but this time without A. fabae. Having done this, the results are not markedly affected, although even alternating species now showed a significant negative relationship between variability and the corrected measure of polyphagy at one of the sites (Silwood Park) (see Table 3a). Results for

Figure 6. Standard deviation of the log-transformed yearly counts versus the degree of polyphagy corrected for abundance for alternating (open circles; dashed regression line) and non-alternating (solid circles; continuous regression line) species of aphid at Silwood Park, England. (Polyphagy was corrected for abundance by taking the residuals about the regression line for the relationship between measures of polyphagy and abundance - see text.)

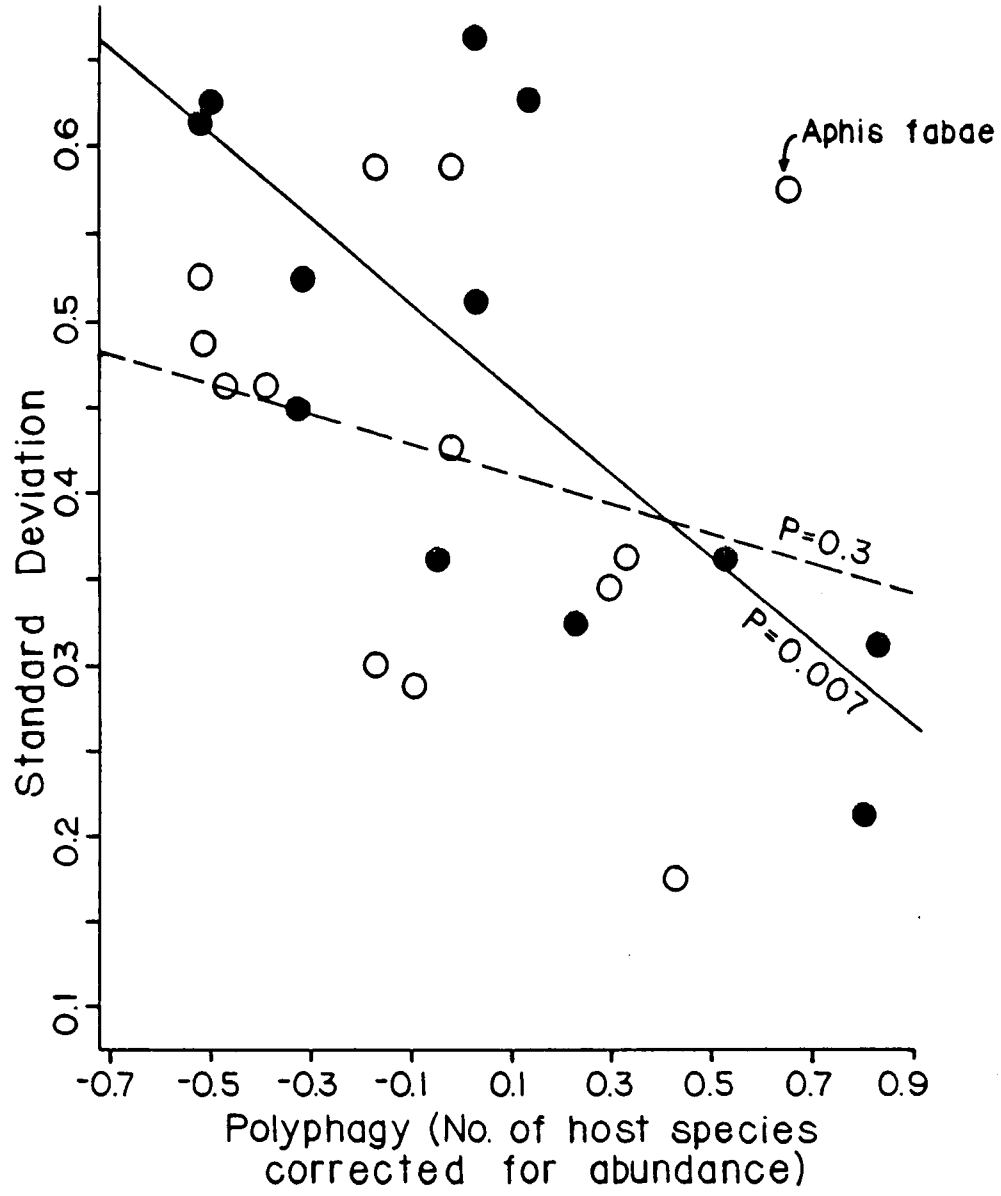
Aphis fabae
P=0.3
P=0.007
Standard Deviation
0.1
0.2
0.3
0.4
0.5
0.6
-0.7
-0.5
-0.3
-0.1
0.1
0.3
0.5
0.7
0.9
Polyphagy (No. of host species corrected for abundance)

Figure 6

TABLE 3 a) Summary of the overall results. For British aphids and Canadian Macrolepidoptera I give the slope and significance level (P) for the relationship between variability (corrected for abundance, where appropriate) and polyphagy (corrected, where appropriate). Aphis fabae was not included in this analysis of British aphids. For British moths I show the results of an analysis of variance, with variability as the dependent variable and degree of polyphagy as the independent variable. b) Results from two other studies. I show the slope and significance level (P) for the relationship between variability and polyphagy. Both studies used log-transformed data: Watt and Craig (1986) used the standard error of this data; Rejmanek and Spitzer (1982) used the coeficient of variation.

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a) Summary of my results

BRITISH APHIDS

LIFESTYLE	SITE	SLOPE	P
Non-Alternating	Elgin	-0.2291	0.1470
	Dundee	-0.2590	0.0117
	Newcastle	-0.1806	0.0395
	High Mowthorpe	-0.0512	0.6307
	Silwood Park	-0.2399	0.0025
	Wye	-0.1002	0.1884
Alternating	Elgin	-0.1310	0.4914
	Dundee	-0.0664	0.6287
	Newcastle	0.1091	0.4194
	High Mowthorpe	0.0023	0.9863
	Silwood Park	-0.2380	0.0236
	Wye	-0.0673	0.5197

Table 3 (continued)

BRITISH MOTHS

DEGREE OF POLYPHAGY	MEAN STANDARD DEVIATION	P
Relatively Specialized	0.4305	0.0217
Intermediate	0.2361	0.3828
Relatively Polyphagous	0.2835	

CANADIAN MACROLEPIDOPTERA

LIFESTYLE	FAMILY	SLOPE	P
Gregarious	All families	0.0358	0.9061
Solitary	All families	-0.0061	0.8341
Geometridae		-0.0504	0.2387
Lymantriidae		0.1799	0.1250
Noctuidae		-0.0124	0.8658
Notodontidae		-0.1511	0.3848

b) Results from two other studies

CANADIAN MOTHS ON DOUGLAS FIR: WATT AND CRAIG 1986)

SLOPE	P
-0.016	0.3181

NOCTUID MOTHS IN BOHEMIA (REJMANEK AND SPITZER 1982)

SLOPE	P
Positive	< 0.005

alternating species were still far less conclusive than those for non-alternating species (see Table 3a).

These results are not significantly altered if I assume that abundance is not a confounding variable and view the uncorrected estimates of polyphagy as being the most important. High variability still tended to be associated with low estimates of polyphagy. In non-alternating species, four of the six sites (Dundee, Newcastle, Silwood Park and Wye) showed a significant negative relationship between variability and the uncorrected measure of polyphagy. Alternating species again showed no clear pattern.

(b) British moths

I found no significant effect of mean log abundance on variability ($P=0.66$) or on the degree of polyphagy ($P=0.35$). Therefore, the analysis was relatively simple: an analysis of variance on the uncorrected estimates of variability grouped by the three classes of polyphagy. Fig. 7 shows that the most

Figure 7. Standard deviations of log-transformed counts for three groups of moths in Britain. Species in group 1 are "relatively specialized", those in group 3 are "relatively polyphagous" and species in group 2 are "intermediate".

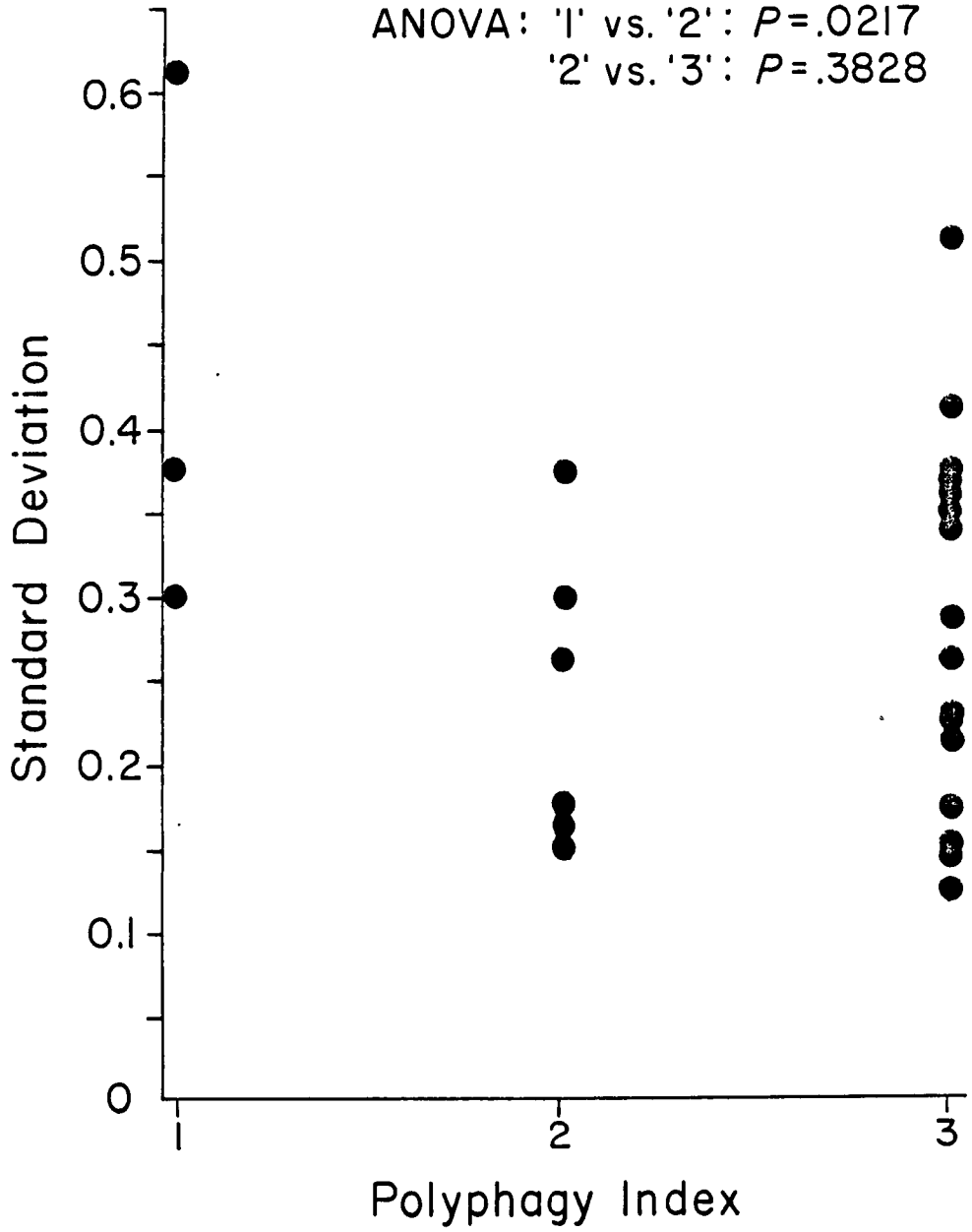
ANOVA: '1' vs. '2': P=.0217
'2' vs. '3': P=.3828
Standard Deviation
0.6
0.5
0.4
0.3
0.2
0.1
0
1
2
3
Polyphagy Index

Figure 7

specialized species were significantly more variable than species in the intermediate group, but that these showed no difference from the highly polyphagous species. (The most specialized species were also significantly more variable than the highly polyphagous species; P=0.05.) Unfortunately, there were only three species belonging to the most specialized group. (Perhaps this is because moths of economic importance are likely to be those that feed on a wide variety of plants). Furthermore, Operophtera fagata Scharfenberg, one of the three specialized species, is particularly variable; the remaining species in this group are well within the range of the points from the other two diet-breadth groups (Fig. 7). According to Skinner (1984), O. fagata larvae feed on plum and cherry, Prunus spp., Apple, Malus sylvestris Mill., and on birch, Betula spp., i.e. on two families of hosts (Rosaceae and Betulaceae). Authors who account for the degree of relatedness of host species in their measure of polyphagy (Rejmanek and Spitzer 1982) would call O. fagata fairly polyphagous,

even though few host species were cited. If I had done this, I would have detected no difference between the specialized species and the intermediate species (P=0.63). Thus, I am less confident in this result than I would like.

(c) Canadian Macrolepidoptera

There was a significant positive relationship between mean log abundance and the logarithm of the number of host genera (P=0.0001). I took the residuals about this regression line as the corrected measure of polyphagy (see Appendix III of Redfearn and Pimm 1988). The relationship between variability and mean log abundance for solitary larval feeders was significantly different to that for gregarious larval feeders (P=0.01). For gregarious species, there was no relationship (P=0.23), and for solitary species, there was a marginally significant positive relationship (P=0.09). Thus, I treated the solitary and gregarious species separately and corrected variability for abundance in solitary species only (see Appendix III of Redfearn and Pimm

1988).

In gregarious species there was no relationship between variability and polyphagy corrected for abundance (Table 3a). In solitary species there was no relationship between variability corrected for abundance and polyphagy corrected for abundance (Table 3a). Again, I must ask, are the results significantly altered if one assumes that abundance is not a confounding variable and uses the uncorrected measures of polyphagy and variability? Again, the answer seems to be no. The relationship between the uncorrected measures of variability and polyphagy was not significant in gregarious species ($P=0.19$; negative regression slope) nor in solitary species ($P=0.13$; positive regression slope). The difference between this relationship for solitary and gregarious species was marginally significant ($P= 0.06$).

Preliminary analyses suggested that some families of Macrolepidoptera were more variable than others. Perhaps this masks any underlying relationship between variability and polyphagy. The large number of solitary species in our data

set allowed us to perform an analysis that separated the different families of Macrolepidoptera. I restricted this analysis to 166 species of the families Geometridae, Lymantriidae, Noctuidae and Notodontidae. In each of the other families there were less than five solitary species for which I had estimates of variability, mean abundance and the degree of polyphagy.

For the species in these 4 families, there was a significant positive relationship between mean log abundance and the logarithmically transformed measure of polyphagy ($P=0.003$). There was a marginally significant positive correlation between mean log abundance and variability ($P=0.09$). Therefore, I used the residuals about both of these regression lines as the corrected measures of polyphagy and variability.

I performed an analysis of covariance, in which variability was regressed against polyphagy, with the different families incorporated as a discrete variable. Three of the four families showed a negative relationship

between variability corrected for abundance and polyphagy corrected for abundance (Table 3a). The family Lymantriidae showed a positive relationship (Table 3a). These relationships were, however, non-significant in all cases. Again, these results were not altered when I used uncorrected measures of polyphagy and variability.

4. DISCUSSION

(a) A Summary of my Results

I found no evidence to support Watt's (1964, 1965, 1973) argument that highly polyphagous species are more variable than more specialized species. Analyses of three independent data sets involving herbivorous insect populations showed that, where the degree of polyphagy had a significant effect on yearly variability, it was a negative one. Table 3a summarizes the results from analyses where I corrected, where appropriate, for abundance: of 20 cases, increased polyphagy decreased population variability in 15 cases. Certainly, most of the results are individually statistically

insignificant. Eight of twelve aphid studies do not show a statistically significant relationship between polyphagy and variability; results for alternating aphid species are generally insignificant; results for Canadian Macrolepidoptera are insignificant - unlike Watt's (1964, 1965, 1973) results. For the analysis of British moths, my significant result relies on the few specialized species for which I have data.

(b) Alternating and Non-Alternating Aphids

While population variability in non-alternating aphid species tends to be negatively correlated with the degree of polyphagy, the relationship between variability and polyphagy is unclear in alternating species. Probably our measure of polyphagy is inappropriate for the alternating species. For these species, we need to know the extent of polyphagy during each part of the life-cycle, and relate these to levels of variability. It may be that the degree of polyphagy during one part of the life cycle determines overall population variability.

(c) Aphid Migration

It is evident that some species of aphid show patterns of spatial distribution that change from year to year (Taylor and Taylor 1979) and these changing distributions may be due to density-dependent migrations as well as differential mortality in different years (Taylor and Taylor 1979, Taylor 1979). My measures of population variability of aphid species were estimated and compared for each sampling site separately. Thus, a drop in abundance of a given species one year at a particular site may have been due to movement away from that area or to increased mortality.

Whether any effect of the degree of polyphagy on local variability through time is mediated through differential mortality or through differences in migration rates is open to question. A monophagous species is present only in some habitats even when extremely abundant. Therefore, pressure to emigrate from densely populated areas may be stronger than for polyphagous species, which occupy more habitat-types in a given area (see Hanski 1982).

(d) The Nature of the Effect of Polyphagy

A small sample of three specialized species of British moths had significantly more variable regional populations than a much larger sample of polyphagous species. Variability was not, however, significantly different between intermediate and highly polyphagous species. Perhaps this result should not be surprising. Suppose there are n independent, variable food populations with the same expected means. The coefficient of variation of the sum of these populations scales with $n^{-1/2}$. Predator abundances might be expected to vary approximately with the sum of the abundances of its prey species. Therefore, adding one more food item to a polyphage's diet has much less effect than adding this to a monophage's diet.

(e) Problems with my Analyses

My analyses largely excluded rare species. I excluded all species that were collected fewer than ten times. Furthermore, the Rothamsted data that I used to analyze British moths and aphids only include species of economic importance. A rare species is less likely to be

economically important than an abundant one, even if both feed on economic plants. Thus, my bias towards abundant species was unavoidable. There is, however, a good statistical reason for excluding rare species. Rare species can not help having low variability (even after we logarithmically transform the data) for purely statistical reasons (Wolda 1983). Even if I had been able to obtain reliable variability estimates for rare species, there would have been a good case for not including them.

I have already aluded to the problem of quantifying the degree of polyphagy (see 'Results' section for British moths). First, data on host records are inevitably incomplete: not all the host plants of many insects are known. Second, it is not usually known exactly how many potential host species are actually used locally (Fox and Morrow 1981). Third, there are a number of different ways of estimating the degree of polyphagy from host plant data (Fox and Morrow 1981). I simply counted the numbers of types of host plants, always using the highest resolution possible from the data source. For

example, I counted host species of British aphids. Rejmanek and Spitzer (1982) categorized insect species according to whether they feed on one plant genus, one family, two to three families or more than three families. An insect species that feeds on two species in different families was, thus, considered to be more polyphagous than an insect that feeds on two closely related host species. Both methods leave out some of the available information provided by host records. I chose my approach because I felt that the higher the degree of resolution used, the more likely that I would be able to distinguish between the two hypotheses (MacArthur's and Watt's) to be tested.

Like Wasserman and Mitter (1978), I believe that, on the whole, any significant trends we detect are likely to occur inspite of, rather than because of, inaccuracies in polyphagy estimates. It is impossible to judge whether my significant result for British moths is an exception.

(f) The Results of Two Other Studies

(i) A limited analysis of Canadian moths

Watt and Craig (1986) have recently analyzed data on five medium-sized Canadian moth species, all of which are solitary leaf-defoliators, have similar ranges, and share Douglas Fir, Pseudotsuga menziesii (Mirb.) Franco, as their principal host. Moth species with few other host species besides Douglas Fir tended to be more variable than the species with many alternative hosts, although this relationship was not significant (Table 3b). Thus, once confounding factors were removed as much as possible, the degree of host specialization did not affect population variability.

(ii) Noctuid moths in Bohemia

We can not ignore Rejmanek and Spitzer's (1982) results for Noctuid moths in south Bohemia. In this case, the degree of polyphagy was significantly positively correlated with variability (Table 3b). The reason why south Bohemian moths should show a positive relationship between polyphagy and variability while British aphids and (less convincingly) British moths show a negative relationship remains a mystery. Rejmanek and Spitzer's result

is not an artifact caused by any confounding effects of abundance. Rejmanek and Spitzer, as a preliminary step in their analysis, had reduced the number of species analyzed from 142 to 72 by excluding all exceptionally rare species. This prtecaution ensured that any dependence of variability on abundance was removed. Furthermore, I repeated their analysis and found that their measure of polyphagy was unrelated to abundance.

(g) An Alternative Hypothesis

John Lawton (personal communication) has suggested a mechanism that differs from MacArthur's (1955), to explain why polyphagous species might be less variable than host-specialist species. This argument involves body sizes and population growth rates. At least in certain groups of Lepidoptera, large species tend to be more polyphagous than small species (Wasserman and Mitter 1978). Large species tend to have lower potential population growth rates (Southwood 1981). For example, large aphids have lower reproduction potentials than small ones (Llewellyn and Brown 1985).

Theoretically, the relationship between population growth rates and population variability may be either positive or negative (Turelli 1978, 1986, May et. al. 1978). For birds (Pimm 1984b) and fish (May et al. 1978) the relationship has been found to be negative. But for noctuid moths, the species with the greatest fecundity and highest potential rates of increase were the most variable (Spitzer et al. 1984). Thus, the degree of polyphagy may affect variability indirectly, via the effects of body size and population growth rates. While this mechanism differs from that suggested by MacArthur, its effects do not. Consequently, my results do not separate Lawton's and MacArthur's hypotheses.

(h) Implications

Table 3 summarizes my results, along with those of Watt and Craig (1986) and Rejmanek and Spitzer (1982). Out of 22 studies, only six show significant correlations between variability and polyphagy. Of these six, only one correlation was positive.

My results (Table 3a) lend some support to

MacArthur's (1955) argument that populations of generalist feeding species may be less variable because they are less susceptible to population reductions during unfavorable years.

I certainly found a lack of evidence for a positive correlation between variability and polyphagy. I do not, however, wish to imply that Watt's (1964, 1965, 1973) argument for this correlation is invalid in all cases. Rejmanek and Spitzer (1982) found evidence for this positive correlation in south Bohemian moths. Variability may be the result of an interaction between life-history characteristics (such as the degree of food specialization) and the degree of environmental stability (Rejmanek and Spitzer 1982). In certain environments, overall variability may reflect the ability to fully exploit rare favourable conditions by rapid population growth (Watt 1964, Redfearn and Pimm 1987). Highly polyphagous species may be best suited for that exploitation.

Watt's arguments may be particularly relevant when one is simply considering outbreak-frequency rather than overall

variability. For example, in a plant polyculture, a polyphagous species is likely to spend less time searching for suitable food plants, reach higher levels faster, and therefore, attain outbreak levels more frequently than a monophagous species in the same situation (Watt 1964). In this context the arguments of Watt have obvious similarities to Root's "resource concentration hypothesis" (Root 1973, Risch et al. 1983), which explains why monophagous,but not polyphagous, insects have reduced densities in plant polycultures compared to monocultures.

I have found a limited number of studies that suggest a negative relationship between population variability and the degree of polyphagy in insects. In such cases, it seems that changing resource levels may cause fluctuations in abundance, the magnitude of which being modified by the range of food plants exploited. There is, however, a widely held belief that regulation from above by predators and parasites is more important in insect populations than is regulation from below by

resources (Strong et al. 1984, Lawton and Strong 1981). We may thus expect a stronger relationship between variability and the degree of susceptibility to predation and parasitism. Certainly, there is enough unexplained scatter around the regressions of variability on polyphagy for this possibility to remain. It is the effect on population dynamics of interactions between herbivorous insects and their natural enemies that I need to investigate next.

IV. THE TEMPORAL VARIABILITY OF SPECIES DENSITIES

1. INTRODUCTION

Ecologists use the term 'stability' to mean a number of different things (Pimm 1984a). One use is to equate stability with low variability in population density over time (henceforth, temporal variability). Temporal variability varies greatly from species to species, so what affects it? There are at least three sets of factors: the variability of extrinsic, abiotic factors, food web structure, and the intrinsic features of the species themselves. We can measure temporal variability using at least three statistics: the coefficient of variation of density (CV); the standard deviation of the logarithms of density (SDL); and the variance in the differences between logarithms of density for pairs of consecutive years (called annual variability, hence AV, by Wolda 1978). There are advantages and disadvantages to each measure (Williamson 1984), though in my experience, the measures are strongly correlated across sets of

taxonomically related species. The increasing availability of long-term data sets allows one to calculate these statistics for many species and so to begin to understand the various causes of species differences in temporal variability.

2. THE VARIABILITY OF THE ENVIRONMENT

Temporal variability will depend on the variability of the abiotic factors that directly determine a species' survivorship and reproduction. We might expect a population's temporal variability to be higher where key abiotic variables are themselves more variable. British bird populations, for example, have densities determined, in part, by the severity of cold winters (Pimm 1984b). So we might expect communities experiencing more variable abiotic conditions to have species whose densities are similarly more variable. Malicky (1976), for example, found that the numbers of emerging caddisflies were more variable from year to year in a stream that varied in temperature from 0 to 19°C, than in a nearby similar one that varied from only 6.0 to 6.3°C. Similarly, McGowan and

Walker (1985) noted the high similarity of species composition of plankton samples taken years apart from the Central Pacific Gyre. The Gyre is a gently-circulating, well-mixed body of water. These high similarities contrast with the low similarity of plankton samples taken only hours apart from turbulent areas in the California current. Salinities were much more variable in the Current than in the Gyre.

Not all such comparisons succeed. Wolda (1983) tested Elton's (1958) assertion that tropical species have populations that fluctuate less (are "more stable") than those of temperate species. Using data on a variety of insect taxa, Wolda concluded that "tropical insects are about as stable, ...as temperate insects, even insects from a relatively undisturbed tropical forest".

Pimm (1984b) suspected that resident species of British birds, which experience occasional hard winters, should be more variable than migrant species. For what ever reasons, migrant species are marginally more variable than resident species.

3. FOOD WEB EFFECTS

While changes in physical variables may affect a species' density directly, they must also affect density indirectly by changing the density of the species' food supply, competitors, predators and parasites, and mutualists. We should expect the patterns of interactions within a community, i.e. the food web, to affect population variability. Comparisons have involved different systems of putatively different food web complexities: tropical systems versus simple temperate systems and natural systems versus simple agricultural systems. These systems differ in ways other than just complexity, however, and so differences in population variability may be due to other causes. As already noted, there do not appear to be obvious differences in variability between tropical and temperate populations. Insect species in agricultural systems, however, do appear to be more variable than those in forest communities (Wolda 1983, Rejmanek and Spitzer 1982).

An alternative way to explore the role of food web structure on temporal variability is to consider the arguments that relate temporal variability to the diet breadth of a species. MacArthur (1955) argued that species exploiting many food species should be less temporally variable than more specialized species. If one food species failed, then a polyphagous species could switch to alternative supplies, while a more specialized species could not. In fact, host switching is not necessary for this argument. Some polyphagous insect species may be composed of separate sub-populations that each specialize on different local hosts. The failure of one of these hosts may severely affect the sub-population, but the total population may be little affected.

Interestingly, Watt (1964) suggested a diametrically opposite affect to MacArthur's. Consider species that are usually rare -- held there by inclement conditions or effective predators. During rare favorable conditions, polyphagous species have the potential to exploit a larger proportion of the environment and to

spend less time searching for suitable resources than specialized species. Thus, polyphagous species may increase more rapidly, attain higher densities, and so be more temporally variable. Specialized species living in monocultures of their prey will also be able to increase quickly and be highly variable. (Perhaps this explains why insect herbivores in agricultural communities are so variable.)

These two opposing arguments are summarized in Fig. 4. MacArthur's idea relates to the effects of deviations below the norm (crashes), while Watt's idea relates to deviations above it (outbreaks). There may be data to support both MacArthur's and Watt's arguments. For aphids and moths in Britain, I (Redfearn and Pimm 1988) have found either no correlation or negative correlations between temporal variability and the degree of polyphagy (Fig. 8a and see Fig. 6). Rejmanek and Spitzer (1982) found a positive correlation between temporal variability and the degree of polyphagy in Noctuid moths in South Bohemia (Fig. 8b).

Parallel arguments may be applied to the

Figure 8. Two opposing results for variability versus polyphagy . a) 26 species of British aphids analyzed by Redfearn and Pimm (1988) and collected by the Rothamsted Insect Survey at Silwood Park, England and b) 72 species of South Bohemian Noctuid moths analyzed and collected by Rejmanek and Spitzer (1982). Variability is measured as the standard deviation of the $\log_{10}(N_t)$, where N_t is the annual density in year t, calculated over a) 14 to 16 years and b) 12 years. Polyphagy is estimated a) by the logarithm of the number of recorded host plants (Redfearn and Pimm 1988) and b) as the following categories: 1-on one plant genus, 2-on one family, 3-on two to three families, and 4-on more than three families of plants (Rejmanek and Spitzer 1982). Small, solid circles are individual species, large circles are the superposition of two (solid) or three or more (open) species. Fig 6. is similar to Fig 8a, but in Fig. 6 variability was measured as the standard deviation of the $\log_{10}(N_t+1)$, polyphagy was corrected for abundance, and two aphid lifestyles (alternating and non-alternating - see section III 2(c)(iii)) were separated.

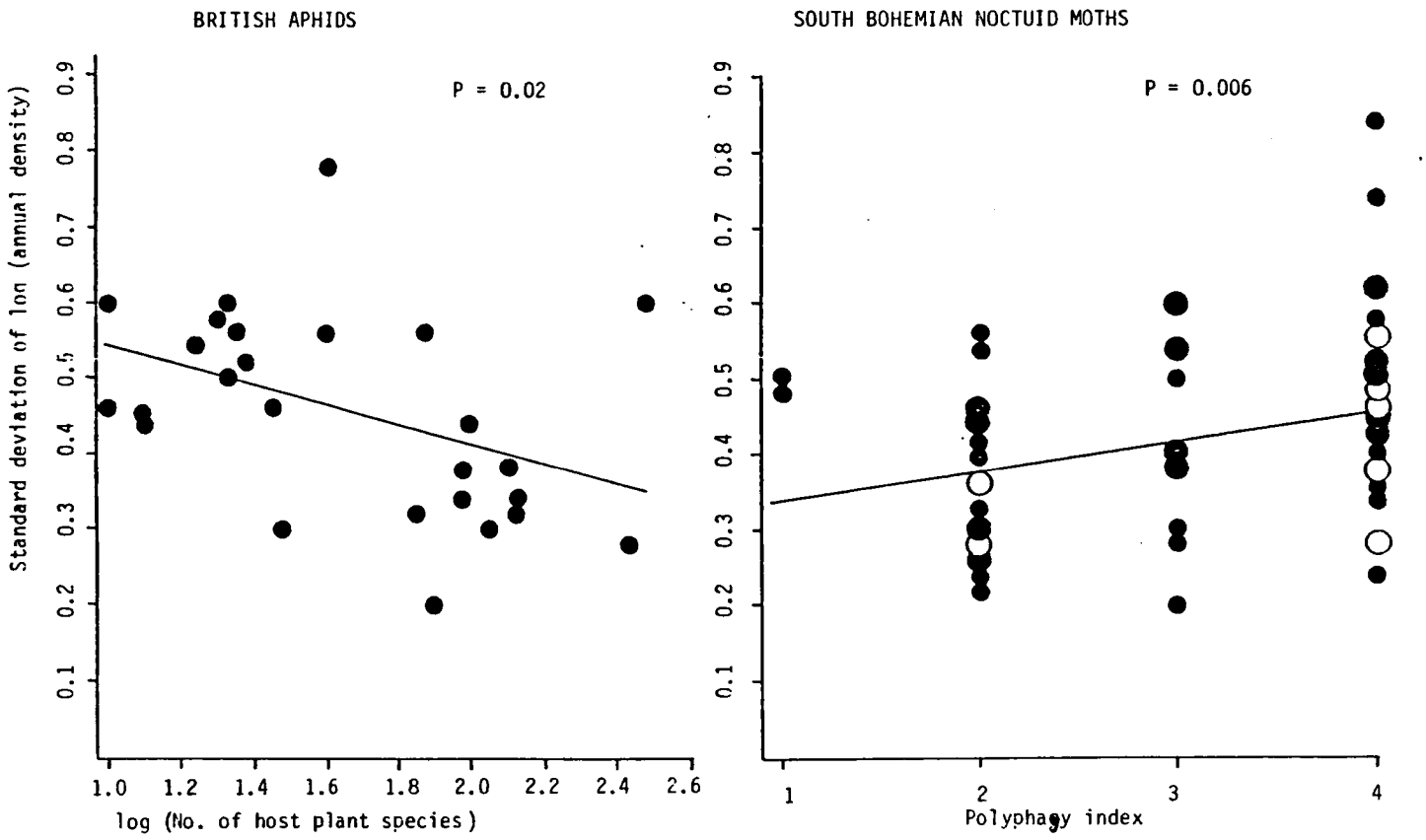
BRITISH APHIDS
P = 0.02
Standard deviation of lon (annual density)
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
log (No. of host plant species)
SOUTH BOHEMIAN NOCTUID MOTHS
P = 0.006
1
2
3
4
Polyphagy index

Figure 8

diversity of predators a species suffers: more diverse communities might be predicted to provide more reliable control of a set of prey species, which would then have less variable densities. Hansson and his colleagues (Hansson 1987, and see review in Hanski 1987) have shown that voles (Clethrionomys and Microtus species) are more variable in the north of Scandinavia than in the south. High variability is associated with multi-annual cycles, which, moreover, are synchronous across species, including insectivorous shrews and birds. These latitudinal differences, Hansson argues, stem from there being only one important (and specialized) vole predator in the north (the least weasel, Mustela nivalis). In the south,there are a variety of generalized predators (e.g. the fox, Vulpes vulpes). These predators, though important to the voles gain most of their food from other herbivores (e.g.rabbits, Oryctolagus cuniculus). Thus, it is the greater diversity of predators in the south that ultimately result in the voles being less variable there.

4. INTRINSIC SPECIES DIFFERENCES

Species differ in many ways that could affect the responses of their densities to abiotic variables and the densities of the species with which they interact. One approach to investigating these species differences is to examine the relationship between body size and temporal variability. I have assembled 202 previously published population studies of terrestrial animals that were conducted at least annually and for at least 15 years. The data comprise 116 bird studies 43 mammal studies and 43 insect studies. The majority of the bird data were collected by the British Trust for Ornithology's (B.T.O) Common Bird Census and are published annually in Bird Study. The data were supplied to us by the Trust's director, R.J. O'Connor. Many of the insects are British moths and aphids collected by the Rothamsted Insect Survey. Most of the remaining studies were used or referred to by two other comparative studies of population dynamics (Tanner 1966, Peterson et al. 1984). Finally, 19 miscellaneous studies were assembled by Stuart L. Pimm's graduate

ecology class of 1986. Both references and data for all but the B.T.O. studies are available on request on IBM-compatible 5.25" discs.

I have calculated three indices of variability (CV, SDL, AV) for each population over just 15 years. Temporal variability increases continuously as more years of data are included in the estimate of temporal variability.

Whatever measure of temporal variability, small-bodied species were significantly more variable than large-bodied species ($P < 0.0001$, in all cases; Fig. 9). This correlation was probably anticipated by most of my readers, but it is not inevitable, nor is its explanation obvious. The correlation may be due to body size directly or through correlations of body size with reproductive rate, longevity, or other factors.

(a) Body Size

Small-bodied species may be more vulnerable to inclement weather and so be more temporally variable than large-bodied species (Lindstedt and Boyce 1985). Data on the percentage decline of British bird species, of various body sizes,

Figure 9. Three measures of population variability versus body weight. All estimates are calculated for 15 years of estimates of annual density, N_t. AV is the variance of $(\log_{10}(N_t)-\log_{10}(N_{t+1}))$, CV is the coeficient of variation of the N_t, and SDL is the standard deviation of the $\log_{10}(N_t)$. Small circles are individual species, large circles are the superposition of three or more species. Solid circles are species that show pronounced cycles of abundance. Solid regression lines are for all the species, dashed regression lines are for species weighing less than 0.1 Kg: such species might be expected to have life spans of about a year or less.

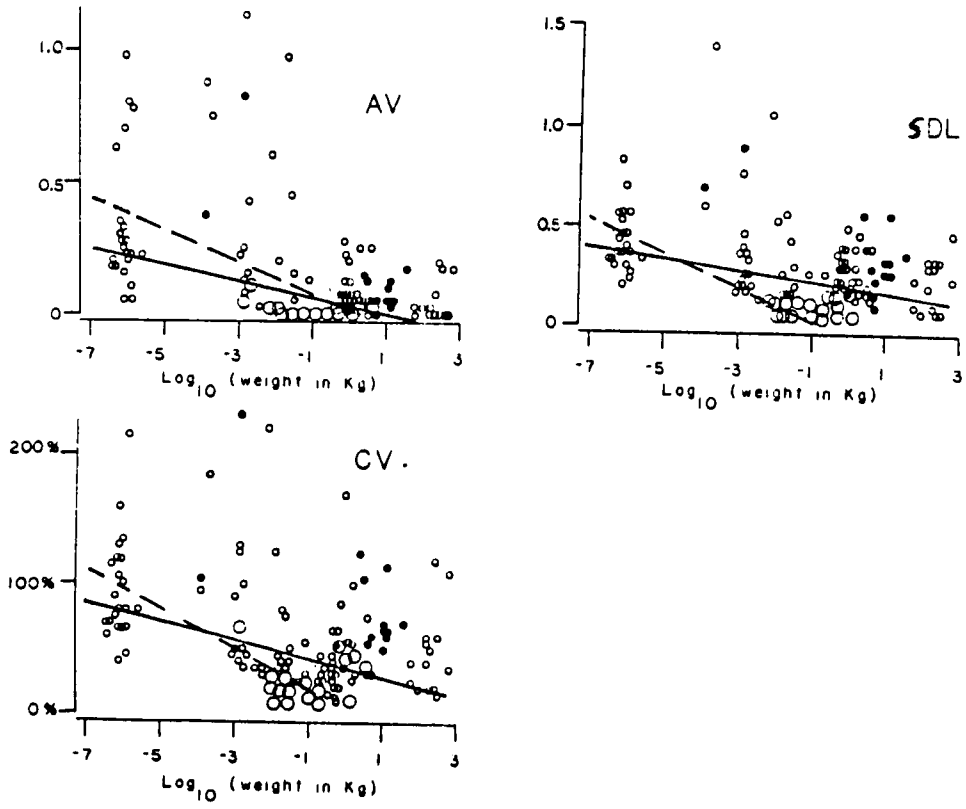

Figure 9

during hard winters support this idea (Cawthorne and Marchant 1980).

(b) Rate of population increase

The rate of population increase, r, has a strong correlation with body size (Southwood 1981): large-bodied species have low rates of increase. Rate of increase may affect temporal variability in diametrically opposite ways (Pimm 1984b).

(i) Populations with high r will recover from population crashes more rapidly than those with low r. Thus, following the same initial decline, high r populations will spend less time at low densities and may, therefore, be less variable than low r species. This relationship holds for British bird populations (Pimm 1984b), in which temporal variability depends on the decrease in abundance following hard winters and the rate at which normal abundances are recovered.

(ii) Populations with high r may be more temporally variable than those with low r, for one of two reasons. 1) If there are time delays in mortality and natality, populations with

sufficiently high r may first overshoot, then undershoot equilibrium, leading perhaps to simple two-point cycles, or to much more complicated dynamics as r increases (May et al. 1978).

In my collection of population studies, obviously cycling species were not always small-bodied (hence high r). But, cycling species tended to be more temporally variable than non- cycling species of the same body size (Fig. 9). This suggests that if high r causes cycling and this contributes to high temporal variability, the effects are independent of, and additional to, the main effect of body size in determining temporal variability. Small-bodied species are highly variable even when no cycles are apparent.

I have an important caveat: many of the populations may show simple cycles, but these may not be apparent in only 15 years of data. (Many of the species for which I detected simple cycles were counted for much longer than 15 years.) Nor can I exclude the possibility that populations show complex, yet deterministic changes of density; the analyses of Schaffer and

Kot (1986) show that such populations may be much more common than once thought.

2) The second reason for a positive correlation between reproductive rate and temporal variability, involves our supposing that the equilibrium density of a population is itself variable. Species with high r will track this variable equilibrium, while populations with low r will respond more slowly, and not tend to track the equilibrium. This possibility may hold for Noctuid moths, in which high r species are the more variable (Spitzer et al. 1984). (This is the opposite result to that I have discussed for British birds.)

Whether one finds a positive or a negative correlation between r and temporal variability may reflect the time-interval between counts and the time over which the population is counted relative to the life-span of the organism, as much as species-to- species differences. Thus, we would expect all populations to track very long-term environmental changes, and to have corresponding changes in density. Over short periods, high r populations may track better than

low r populations, and so low r populations will vary less. And over intervals dominated by rare, but severe population crashes, high r species will vary less.

(c) Longevity

Large-bodied species also tend to be long-lived (Bonner 1965), so large-bodied species might be expected to vary less in density, because, in the extreme, it may be the same individuals that are counted in each of the years of the study. In contrast, small-bodied species may have gone through several generations in each of the years. A hypothetical population of adult redwood trees might show no density variation at all over, say, 15 years! In order to evaluate this effect, we would need to calculate temporal variability from generation to generation rather than from year to year. There is a simpler alternative though. Animals that weigh less than 0.1kg (small birds, small mammals and insects) are likely to complete their lives within a year, or to have generation times on the order of a year (Bonner 1965). The negative relationship between temporal variability and

body size not only holds for this subset of the data (Fig. 9), but the associated regressions have even more negative slopes than for the combined data. For this subset, the different years of data must generally involve different individuals, and so large-bodied species averaging out fluctuations cannot be the reason for why there is a negative correlation.

(d) Other factors

Small-bodied species may be more variable because they are more specialized than large-bodied species. This seems the least likely explanation for the overall negative correlation. First, as I have already mentioned, polyphagy does not necessarily decrease variability, and when it does, the correlation is rarely a strong one. Second, although within taxa, large-bodied species tend to be more polyphagous (Wasserman and Mitter 1978), it seems unreasonable to suggest that mammals are less variable than insects because they are sufficiently more polyphagous than insects.

There must be many other correlates of body size that also affect temporal variability.

However, the species that contribute to the relationship in Fig. 9 are diverse both trophically and taxonomically. The very smallest species (aphids) are herbivorous as are the very largest species, (mammals). So the negative relationship is not due to trophic differences.

V. VARIABILITY OF POPULATION DENSITIES

1. INTRODUCTION

The variability of population densities over time (henceforth called population variability) is one of several meanings of ecological stability (Pimm 1984a). Here I show that estimates of the variability of population densities increase as I increase the number of years included in their calculation. This result appears for the majority of populations surveyed and over almost all the time intervals over which I calculate the variability. This result has implications for the debate over whether populations have an equilibrium.

My analyses of population variability are motivated by a recent suggestion that, if correct, has profound implications for ecological theory: Steele's "red-noise" metaphor (Steele 1985). Steele demonstrates that spectral analyses of time series of physical variables in the ocean are reddened: amplitudes increase approximately as 1/(frequency). For example, temperature changes in the deep ocean have a

spectrum which shows continuous increases in amplitude as the period (inverse of frequency) increases from hours to years. Sea level changes have a spectrum where amplitude increases as the period increases up to a million years. Variation of these variables can be modelled approximately by adding a series of sine waves, with amplitudes increasing with decreasing frequency and with random phases (Fig. 10). This reddened spectra also implies a characteristic fractal dimension to the time series (Rothrock and Thornike 1980).

Now, Steele argues that, over short time scales, the spectra of terrestrial, physical variables appear white (all amplitudes are equal). For example, Steele argues that atmospheric temperature records give a spectrum in which all amplitudes are equal up to periods of about 50 years. Williamson (1981, 1987), for one, argues that terrestrial systems do have reddened spectra, not only in time, but in space

Figure 10. Population densities and the change in variability with the length of census. At top left, density of the Skylark (Alauda arvensis) in English farmlands is plotted against year: the scale is relative and set to 100 in 1966. At top right, for the same population, variability, measured by the standard deviation of the logarithms of density is plotted against the period over which the calculation was made. For both nested years (2, 4, 6, and 16) or non-nested years (2, 4, and 8) variability increases with period. Pre-1970 densities were ignored because, before 1970 many bird populations were recovering from a crash in 1963 following a hard winter: inclusion of these data would have made the increase in variability even more marked.

Similar data for two model populations are shown at bottom. At left, the two model population densities are plotted against year. The trajectory labelled "red" was formed by summing sine waves with random phases and amplitudes that increase linearly with period. The trajectory labelled "white" was formed by choosing densities randomly with uniform probability over the same range as those densities in the "red" model. At right, variability increases for the "red" population, but not for the "white".

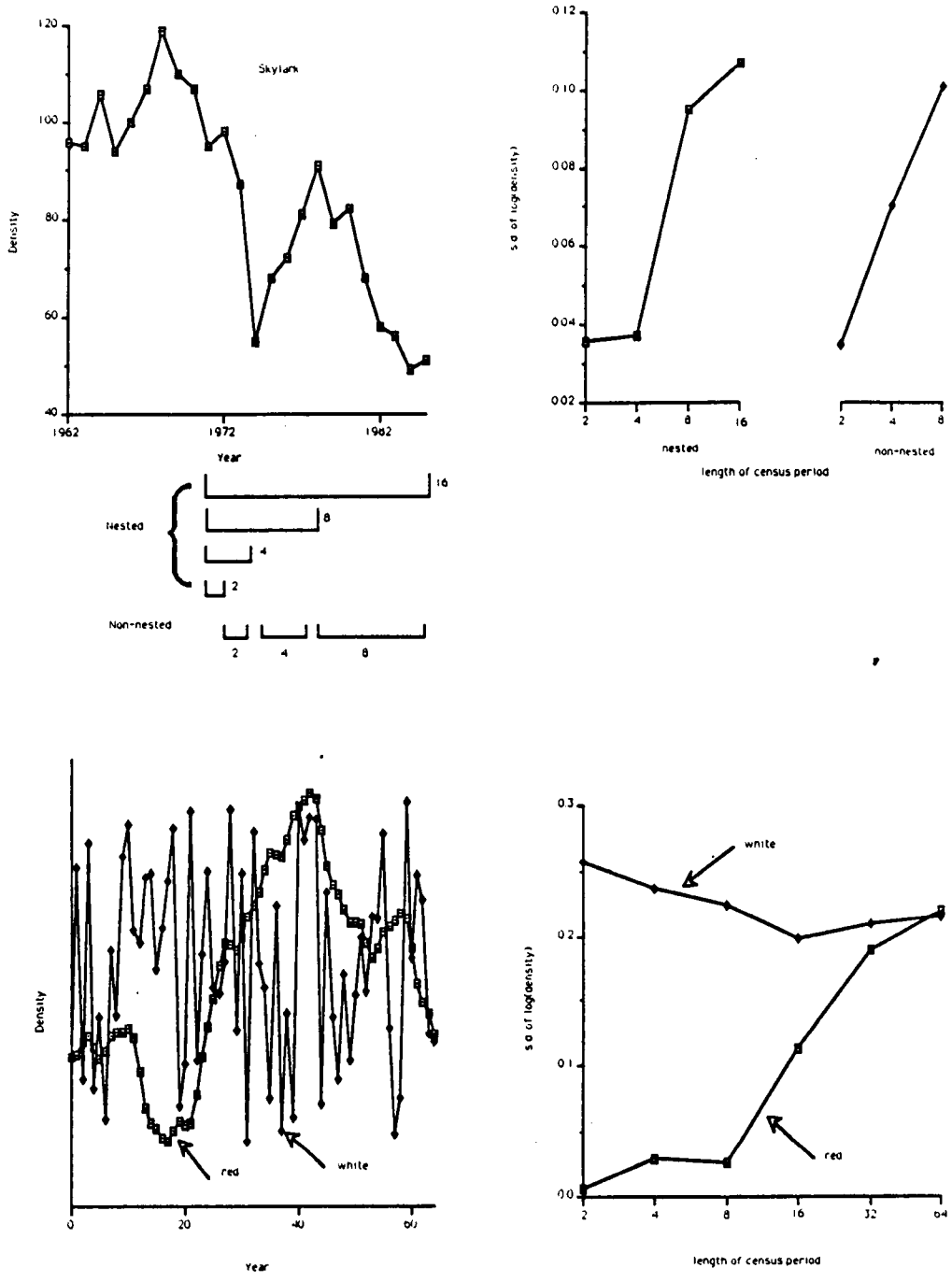
Skylark
Density
Year
1962
1972
1982
Nested
Non-nested
nested
non-nested
length of census period
red
white
Density
Year
length of census period

Figure 10

too. As Williamson (1987) succinctly puts it: "It is a commonplace that the further off in [time and] space, the more different, on average, the environment is". Williamson realized the important implications that the reddened spectra have when asking whether ecological communities are ever stable. The apparent stability of the community may depend on how long (or over how much space) we observe the community.

Suppose that terrestrial physical variables do have reddened spectra and that physical variables force variation in population densities. While population data are rarely long enough for sensible spectral analyses, we can ask what these suppositions mean in terms of how population variability changes over time. Irrespective of the theoretical justification, this is an important empirical question. With "red noise" we would obtain increasing variances of population abundances as we increase the period over which the variances are calculated. What might appear as an average (an "equilibrium") over a few years, is really a level which cycles over a longer time period, and

that cycle, in turn, is moving cyclically on an even more powerful (high amplitude), less frequent cycle (Fig. 10).

2. METHODS

To investigate these ideas I have determined how variability changes with the number of years included in its calculation. From the literature, I have assembled two sets of population studies that might be considered 'best' for my purposes in two different ways. The first set involves the longest studies I could find: 26 terrestrial population studies that were counted at least annually and for at least 50 years (Tanner 1966, Peterson et al. 1984). There are 4 insect species, the rest are birds and mammals. The second set involves species counted over 24 years, all using the same technique and one designed to be the most suitable: the data on breeding densities of birds in British farmlands (42 species) and woodlands (32 species) published annually by the British Trust for Ornithology (Marchant and Hyde 1980).

There are several measures of population

variability (Williamson 1984). I present data for the standard deviation of the logarithms of annual density (SDL). The results for other measures are qualitatively the same.

For the data on British birds, I have calculated SDLs over 2,4,8, and 16 years for the each of the bird species. I have done the same calculations plus additional calculations for 32 and 50 years for the species in the long-term data set (Fig. 11). The choice of the log(2) timescale is arbitrary. In Fig. 11, the calculations are on nested data: the first two years, the first four years, etc. I have also calculated SDLs for non-nested data: the first two years, the next four years, and the next eight years for the woodland and farmland birds. (I would need a total of 30 years to be able to include estimates for SDL across the next 16 years.)

Figure 11. Population variabilities versus the number of years over which those variabilities were calculated. Only standard deviations of the logarithms of densities (SDL) are shown: the other measures of variability show a similar pattern. On each graph the middle line joins the means among the different species; the top and bottom lines join the maximum and minimum values respectively. Regressions of SDL versus the logarithm of time period are all significant at $P < 0.01$. The percentages of these species that show increases between the different numbers of years that go into the calculation are shown in Table 4.

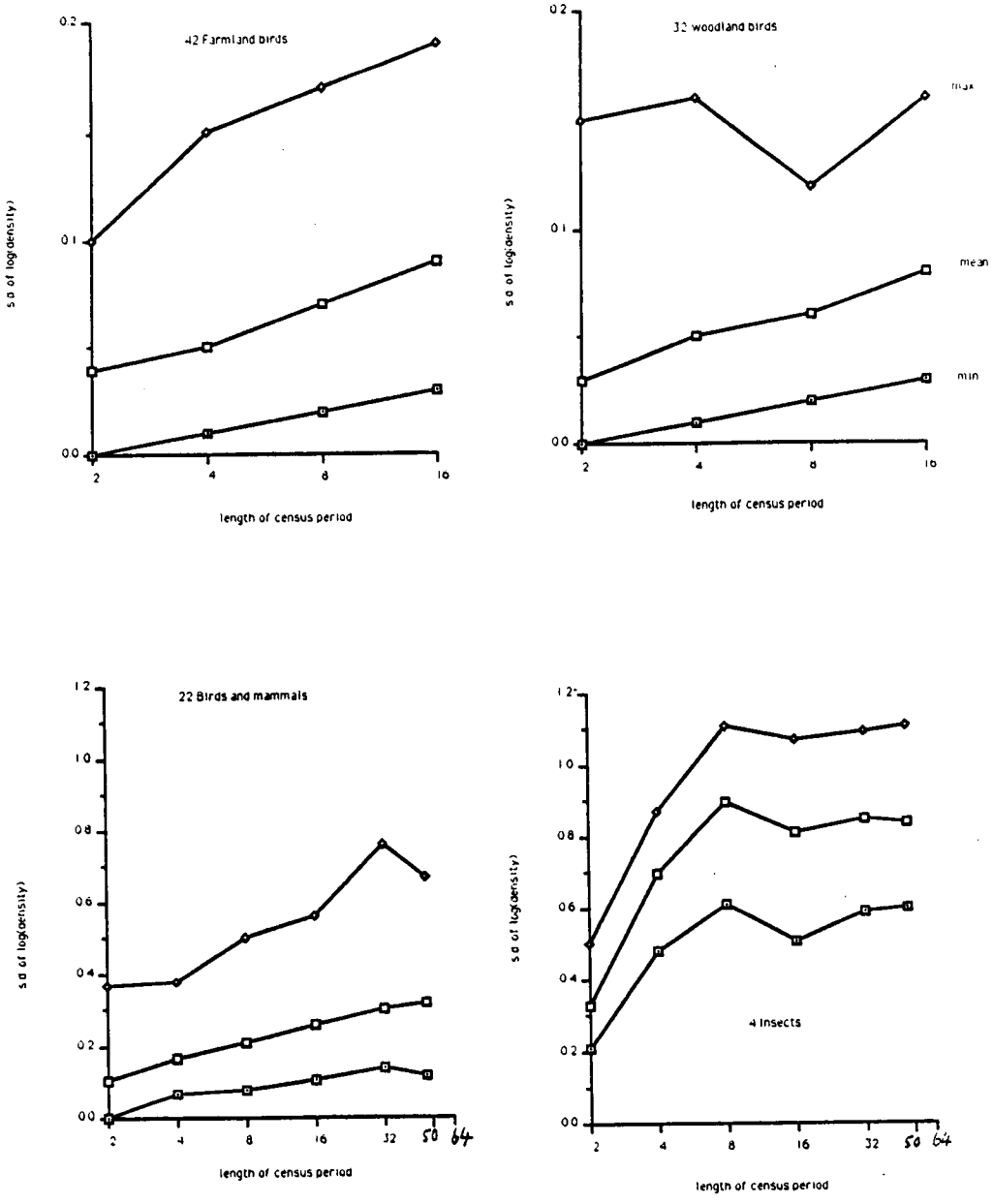
42 Farmland birds
32 woodland birds
22 Birds and mammals
4 Insects
s.d. of log(density)
length of census period
mean
min
0.0
0.1
0.2
0.4
0.6
0.8
1.0
1.2
2
4
8
16
32
50
64

Figure 11

3. RESULTS

Irrespective of the method used, the population variability increases with the length of time over which I calculate it. For the nested analyses, regressions of SDL versus the length of census period are significant at $P < 0.0001$ for the woodland birds, for the farmland birds, and for the 22 miscellaneous birds and mammals; the analysis for the four insect species is significant at 0.008 (Fig. 11). For the non-nested analyses, regressions are significant at 0.0001 and 0.0003 for the farmland and woodland birds respectively.

It is possible that this increase in average variability could be due to a small number of populations with large increases in variability. Consequently, another useful statistic is the proportion of the populations that show increases in variability with the length of the census. The majority of populations show such an increase (Table 4), so rejecting this possibility. (Only for the four species of insect is there not an

Table 4. Percentages of populations that increase in variability over different time spans for the calculation. The years used in the calculations are nested (see text). The measure of variability is the standard deviation of the logarithms of density (SDL).

Comparison of SDLs calculated in these number of years:	2-4	4-8	8-16	16-32	32-50
Farmland birds (42 species)	69[1]*	72**	79**	-	-
Woodland birds (32 species)	72*	75**	72*	-	-
Various birds and mammals (22 species)	68+	68+	77*	55	41
Insects (4 species)	100	75	0	75	25

[1]Thus 29 of 42 (69%) farmland bird species showed greater variabilities when calculated over 4 years versus when calculated over just 2 years. Over all the data we might expect the percentages to average 50% -- half the populations increasing, half decreasing. On this basis, the significance of chi-square tests are given: +<10%, *<5%, and **<1%; sample sizes are too small for the insect populations.

increase, and this is only at the very longest time intervals, when the standard deviation of the logarithms, SDL, levels off at about 1 (Fig. 11). It is possible that a SDL of about 1 is an upper limit consistent with population survival: it is equivalent to approximately four orders of magnitude of density variation over 50 years.)

4. DISCUSSION

This increasing variability would be expected for populations showing simple cycles with wave-lengths at least as long as the longest census period, or, comparably, if there were long term trends in all the data. It is known that some of the populations show pronounced short-term cycles. But only a small number of the species are known to cycle, and this is not a feature of any of the bird populations. In any case, the maximum cycle length is perhaps a decade (for species like the Canadian Lynx), and the populations show increasing variability beyond this.

We might expect some populations to show

long-term trends. For example, all of the populations may have been recovering from some severe, but infrequent disturbance. The British bird populations suffered such a major collapse during the unusually cold winter of 1962/1963. To be conservative I analyzed data from 1970 onwards. Alternatively, many of the populations may have been showing steady declines in abundance. Increasing variance in the bird populations, for example, might be due to degradation of say, British farmlands, with all the populations decreasing for the same reason. But there is no common trend in the species' abundances: some species increase, others decrease. Indeed, the summed densities of all the woodland and farmland species vary by less than +_3% in both cases. The assorted species for which I have 50 years or more of data, are from various countries in different centuries, so a single cause for the pattern of increasing variability seems unlikely.

The conclusion must be that the majority of populations show long-term trends in abundance, for different reasons and hence in different

directions. Moreover, over all the time scales over which I have calculated variability, it is the long-term trends that predominate -- a result strongly suggestive of these population time series having reddened spectra. What are the implications of this result? Ecologists continue to ask questions concerning the existence of ecological equilibria and whether density dependent or density independent processes predominate in determining population densities. Alternative theories suggest, or are suggested by, different levels of variability. Lack, for one, argues that populations are commonly regulated by internal density dependent factors (e.g. competition for limited resources) that return them to a stable equilibrium level. Such populations are not likely to be highly variable. Alternatively, external density independent processes such as fluctuations in the climate may determine population levels, causing large fluctuations in density (Andrewartha and Birch 1954). The results on reddened spectra suggest two ideas.

First, if population time series do have

reddened spectra, and if time series of physical variables have reddened spectra too, then by implication, this suggests that the variability of external physical factors forces the variability of population densities.

Second, density dependent factors may set an average or equilibrium level over a few years, but if physical or climatic variables have reddened spectra then this equilibrium level may cycle over longer periods of time. And that cycle may be moving on an even more powerful infrequent cycle. Any equilibrium level may not be obvious if we have too few years of data. As we accumulate more years of data the equilibrium may have changed, and as we accumulate data, the more important are those changes in equilibrium density.

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