# Top-down versus bottom-up and the Ruritanian bean bug

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**ABSTRACT** In a recent article, Hunter uses the late George Varley and George Gradwell's long-term data on the winter moth (*Operophtera brumata*) and green tortrix (*Tortrix viridana*) populations to propose a method of quantifying the relative importance of top-down effects (because of natural enemies) and bottom-up effects (because of resource competition) in influencing population dynamics. We believe this approach is deeply flawed. Using Varley and Gradwell's winter moth study, we show that the problems with Hunter's analysis lie in his misinterpretation of the population dynamics and his inappropriate use of statistical techniques. We also emphasize the importance of distinguishing clearly between two quite different things: firstly, top-down and bottom-up regulation of populations and secondly, the much simpler task of categorizing factors affecting changes in population density as either top-down or bottom-up processes.

Population ecologists interested in insect herbivores have often argued over the extent to which their population densities are influenced by their food supply (bottom-up effects) or by the action of their natural enemies (top-down effects) (e.g., refs. 2, 3–5). In a recent article, Hunter (1) proposes a methodology to disentangle the relative importance of bottom-up and top-down affects and to assess numerically their relative importance. Although supportive of his aims, we are concerned about the conceptual and methodological basis of this work, issues we explore in this paper. To illustrate the techniques, Hunter uses data collected by Varley and Gradwell, who died in 1983 and 1974, respectively. The late George Varley was something of a stickler for clear thinking over concepts such as "population regulation" and "population control." For example, he castigated ecologists for using "control" in six quite different ways[†] (6); he took issue with Milne (7) over definitions of "equilibrium" and "maximum density" (8) and with Solomon (9) over usage of the term "density dependence" (10). We think that Hunter's paper falls short of Varley's standards of rigor.

Hunter uses Varley and Gradwell's long term population data on two species of moths, the winter moth (*Operophtera brumata*) (11, 12) and green tortrix (*Tortrix viridana*) (unpublished data), at Wytham Wood, near Oxford, England, to illustrate how simple statistical techniques might be used to quantify the extent to which the dynamics of a herbivore are influenced by top-down and bottom-up processes. It clearly would be an important advance if indeed the relative contributions of each could be discerned so readily from time series data. Unfortunately, we should not raise our hopes; Hunter's approach is not the remedy and is likely to be seriously misleading. We first point out flaws in Hunter's interpretation of the population dynamics involved and then discuss how the statistical methodology he adopts is inadequate for the task in hand. Although Hunter examines time series for both winter

moth and green tortrix, we concentrate primarily on the winter moth because much more is known from Varley and Gradwell's work about the biology and population dynamics of this species and because the densities of tortrix decline steadily over the study period, which complicates the interpretation of the data. Our more general criticisms, however, apply equally to both species of moth.

## Basic Biology of the Winter Moth

Varley and Gradwell's winter moth study at Wytham Wood is one of the classic long-term studies in insect ecology (e.g., refs. 11–14). Their census of the winter moth populations began in 1950 and continued uninterrupted until 1968. From these data, they developed their "key-factor" method for analyzing sequences of life table data from organisms with discrete generations and also were able to parameterize a simple model for winter moth dynamics, among the first attempts to do this for any insect population.

The winter moth is a univoltine species. The adults emerge from the soil in November and December, the wingless females then oviposit in the crowns of oak (*Quercus robur*) and other trees. Egg hatch occurs in early April and, after feeding on the leaves of their host-tree, the fifth and final larval instar is reached in May, after which the prepupae spin down to the ground on silken threads and pupate in the surface layers of the soil where they remain until emerging again as adults in the following autumn. Varley and Gradwell studied the winter moth population in a stand of oak trees and, for their routine census data, restricted their samples to five particular oak trees, which were not picked at random; rather they were originally selected in 1949 to represent the range of tree-to-tree larval densities observed in that year (this point is important—we return to it below). Each year, by estimating the numbers of adult females ascending these trees and the total numbers of prepupae descending to the ground to pupate and whether or not these were healthy or affected by a range of natural enemies (by dissection of the samples), they were able to recognize and quantify in each generation a number of mortalities or "disappearances" between stages.

## Problems with the Interpretation of Winter Moth Dynamics

Varley and Gradwell concluded that the "key factor" in their study—the factor primarily responsible for the observed pattern of fluctuations of the winter moth—was their so-called "winter disappearance" ($k_1$), made up of the combined losses

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[†]"Damage by the bean bug is variable in Ruritania, and weather is mainly responsible for its control (*i*), but the level of control (*ii*) on the coast is unacceptable because up to 50% of the crop may be unsaleable. Experiments using DDT to control (*iii*) the pest proved ineffective, even though control (*iv*) was repeated monthly and over 90% control (*v*) was achieved. Pest resurgence was rapid, and the bug population was soon above that in the control (*vi*) area where no insecticide was used." (From Varley (6) under the heading, "*Control of the Bean Bug in Ruritania*." The italicized roman numerals are Varley's and indicate six separate meanings of the word control).

between their samples of newly emerged adult females as they ascended the trees to oviposit and the subsequent counts of total prepupae as they descended to the ground to pupate (Fig. 1*a*). Although this category includes a wide range of factors affecting natality and mortality (e.g., variations in fecundity per adult, predation of eggs by beetles, harvestmen and other predators, bird predation of larvae, and larval parasitism), the major component was thought to be the losses of first instar larvae between egg hatch and becoming established in the opening leaf buds.‡ The other major factor that Varley and Gradwell identified was the mortality of winter moth prepupae and pupae in the soil, largely caused by invertebrate and vertebrate generalist predators (their $k_5$) (15, 16) but also including some pupal parasitism by an ichneumonid parasitoid, *Cratichneumon culex* (their $k_6$). Not only was $k_5$ a large mortality (average of 76% of all healthy prepupae entering the soil to pupate), but it also was unambiguously density dependent (Fig. 1*b*).

It was the interplay of the two factors in Fig. 1 that Varley and Gradwell concluded was driving the winter moth dynamics: the key factor ($k_1$) "buffets" the population around a potential equilibrium rendered stable by the density dependence in the soil. All of the other measured components of the life table had relatively minor affects—predicted winter moth densities were altered little if factors such as parasitism by a microsporidian (*Plistiphora*) and a variety of parasitoids (*Cyzenis*, *Rogas*, and *Phobocampe*) were omitted from the winter moth models.

This quite detailed, mechanistic understanding of winter moth dynamics is in sharp contrast with Hunter's analysis. Hunter claims that top-down (natural enemy) effects make up 34% of the overall variance in population fluctuations. This figure stems from the proportion of the variance (either tree-to-tree or from year-to-year) that he found associated with time delays and from his assumption that these time delays stem from the action of natural enemies. Hunter also claims that 17% of the population variance can be ascribed to bottom-up effects (the remaining 49%, he suggested, is unexplained). This figure comes from the proportion of the variance that does not have time lags, and his assumption that these arise from variations in tree quality. This categorization, however, is at odds with what we see in Fig. 1*b*. Although time delays are associated clearly with the natural enemy-driven soil mortality (in which they are shown by the anticlockwise spiraling), there is also an obvious direct density-dependent component to these data. This will clearly contribute to non-time-lagged variance and yet is unambiguously top-down in its effects.

More generally, the biological logic underpinning Hunter's analysis is suspect. It should not be assumed that immediate density-dependent effects all can be attributed to bottom-up processes and delayed density-dependent effects to top-down. Immediate density dependence can result from top-down processes, e.g., when generalist predators exhibit an aggregative numerical response. Bottom-up processes can produce time-lagged density dependence, e.g., when feeding by caterpillars in year $t$ induces chemical changes leading to reduced food quality in year $t+1$.

In principle, with sufficient biological information, it might be well possible to overcome these serious shortcomings in
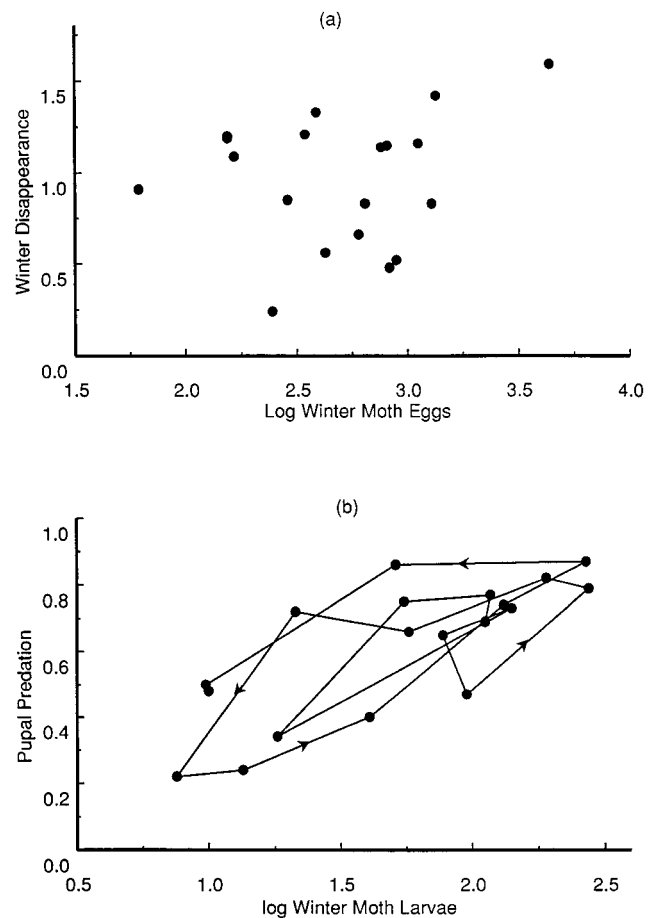


FIG. 1.    Relationships between two of Varley and Gradwell's (13) winter moth mortalities and the corresponding winter moth population density on which they act. The mortalities are expressed as $k$-values (14), where $k = \log_{10}I - \log_{10}S$ and $I$ is the initial density, and $S$ is the density of survivors from the mortality. (*a*) "Winter disappearance" ($k_1$), where $I$ the density of winter moth eggs per m² obtained from the counts of female winter moth ascending the sample trees in the previous November/December, and $S$ is the density of all winter moth larvae descending to the ground to pupate in late May/early June. (*b*) "Pupal predation" ($k_5$), where $I$ is the density per m² of healthy winter moth prepupae, and $S$ is the density of those surviving mortality in the soil (subsequently emerging adult winter moth and the parasitoid *Cratichneumon culex*). The points from 1950 to 1968 are linked serially to show the anticlockwise spiraling that indicates a time-delayed component to this mortality (for further discussion, see text).

Hunter's analysis. But fundamental problems remain in his statistical approach, to which we now turn.

## Problems with the Statistics

The basic data used by Hunter consist of time series of 16 years from each of five oak trees. Hunter uses two-way analysis of variance on the complete data set to partition variance into between-tree and between-year components. For the winter moth, the tree component was 22.6% and the year component 68.4%. Previous experiments by Hunter showed that 76% of the variation in winter moth density between trees could be explained by the date of bud burst. The date of bud burst is significant because the amount and quality of food available to the larvae depends critically on the relative timing of bud burst and egg hatch. Hunter thus allocates 76% of the year component (i.e., 76% of 22.6% = 17.2%; we rounded this to 17% in the previous section) to a bottom-up effect. But of course, as pointed out above, Varley originally chose the five trees in 1949

‡Although never published, Varley & Gradwell found an interesting and significant correlation between the magnitude of the "winter disappearance" of winter moth and the total number of predatory carabid beetles in the genus *Dromius* that they caught over the winter period in their tree trunk traps. If a real effect, this suggests that variations in the year-to-year mortality of first instar larvae at the time of egg hatch might have been less important than fluctuations in the density of these canopy-feeding egg predators.

to maximize the differences in larval density between trees, an effect which later turned out to be consistent throughout the years.

A further problem with the between-tree component is that insect numbers are estimated on just 4 degrees of freedom, but we know from other long-term studies of *Quercus robur* in southern England (e.g., refs. 17 and 18) that there is strong positive autocorrelation across years. Thus, although the repeated measures used by Hunter on the same trees over the duration of the study contain important information about trends in within-tree insect populations, they cannot be used to establish the significance of between-tree differences.

To apportion the year component to top-down and bottom-up factors, Hunter first performs time series analysis on population growth rate ($r_t$) by using averaged data from the five trees. For winter moth, he finds a significant delayed effect of population density that, as we have already noted, he attributes to feedback through natural enemies. Regression analysis shows that mortality caused by pupal predation at time $t$-1 is strongly density-dependent (with $r^2 = 50\%$). Thus, he attributes 50% of the year effect (i.e., 50% of 68.4% = 34.2%; rounded to 34% in the previous section) to top-down effects.

The kind of time series analysis undertaken by Hunter requires that assumptions are made about the way in which the measurements on the five trees are averaged. Using the unweighted mean population in each year requires that the five study trees are a representative sample of the trees contributing to the local insect population. But as we point out above, this assumption is at odds with Varley and Gradwell's intention to select trees with consistently high or low insect infestations. Time series analysis for each of the five trees separately, as carried out by Hunter, also assumes that there is no mixing of the insects across trees between generations. Although rather little is known about the details of dispersal by winged adults or by ballooning early instar larvae, this assumption is highly questionable.

Given this catalog of problems, what approach should be adopted? A thorough analysis of this system must take account of measurement errors, serial correlations, random effects, and structured covariance amongst the explanatory variables. The statistical framework for this kind of analysis is provided by nonlinear-mixed effects models for the analysis of longitudinal data (19, 20). It is clear that there will be year effects, site effects, and year-by-site interactions, none of which are adequately treated by Hunter. One of the major difficulties with the Wytham data is that site effects are completely confounded with tree effects. This matters because some effects are clearly tree-specific (genotypic effects on bud-burst phenology of leaf quality) whereas others are site-specific (rate of predation by generalist predators). A robust approach to the analysis of the Wytham data must take all these issues into account.

A more appropriate model, therefore, might be of the form:

$$X_{i,t+1} - X_{i,t} = a_i + f_{t,i}\left(\sum_{j=0}^{lag}\sum_{k=1}^{5}\beta_{k,t-j}X_{k,t-j}\right) + \vartheta_i t + U_i + Y_t + \varepsilon_{i,t}$$

where $X$ is log density and $i$ and $t$ refer to tree and year, respectively. There are differences in mean population growth from tree to tree (random effects, $U_i$). There are differences in mean population growth from year to year (random effects, $Y_t$). There may be tree-specific trends in mean insect density $\vartheta_i$. There is covariance structure in the error term (autocorrelation and cross correlations in $\varepsilon_{i,t}$). The functional forms $f_{t,i}$ ($\bullet$) relating population change to past densities may differ from lag to lag (e.g., because of ecological differences in the consequences, say, of the immediate impact of generalist predators and the lagged impact of numerical responses by specialist parasitoids) or from tree to tree (e.g., because of differences in average caterpillar density on different trees). In

principle, none of these complexities is insurmountable; although in practice, the amount of biological information required to carry out correctly the analysis attempted by Hunter far exceeds the data currently available for winter moth.

In brief, in Hunter's analyses, there are fundamental problems and/or omissions in all four stages of the model-fitting process: (*i*) in formulation (no explicit model is presented, and no alternatives tested); (*ii*) in parameter estimation (no allowance is made for the structured covariance); (*iii*) in inference (model simplification is not attempted); and (*iv*) in diagnostics (there are none). We therefore conclude that, the biological problems aside, nothing can be deduced from his analyses about the relative strengths of top-down and bottom-up effects because of these fundamental flaws in the statistical methods. However, we do believe that the way to understand problems in population ecology is to take a three-pronged approach, combining mechanistic population models, field and laboratory experiments, and the analysis of observation data by time series analysis and other statistical techniques. We are generally very optimistic about future progress in this area.

### The Bean Bug in Ruritania Revisited: On Getting the Definitions Consistent

A more general failure of Hunter's approach is the lack of clarity over exactly what is meant by top-down and bottom-up "forces" (his word, in the title of his paper) on insect herbivore populations. We suspect that much of the apparent disagreement in the literature in this area reflects workers talking at cross purposes, and so we next digress briefly to make our use of these terms explicit.

Consider an insect population that shows long-term persistence over a particular spatial scale. If we had sufficient data, we could write down a probability distribution describing the expected state of the population at a particular time (21). Because the population is persistent, it must experience density-dependent effects that stop the population increasing to infinity or going extinct (we neglect the pathological case of the intrinsic rate of increase being exactly zero). It is these density-dependent effects that allow us to describe the expected state of the population by a probability distribution. One interpretation of the top-down/bottom-up debate is the extent to which the density dependence that allows persistence is caused by resource competition or natural enemies. Let us call this interpretation the debate over top-down vs. bottom-up *regulation*. Although some species clearly will experience density dependent effects from both resource competition and natural enemies, it is easy to envisage species whose populations are regulated wholly by one or the other. A further point is that not all density-dependent factors contribute to long-term persistence. Especially when density dependence is over-compensating and time lagged; it may then increase the likelihood of the extinction of a species. Where more than one density-dependent factor influences persistence, we are unaware of any statistical technique to partition their relative contributions.

A different interpretation of top-down versus bottom-up is in terms of the factors that influence the fluctuations observed in the population density of a species. Let us call this the debate over top-down vs. bottom-up *influences*. The different factors can be partitioned into those caused by variation in resource abundance and quality (bottom-up), those associated with natural enemy mortality (top-down) and other independent factors, such as the direct effects of the weather. Assessing the relative importance of these different types of factors is essentially a statistical problem, and the appropriate technique will vary from species to species. The most straightforward case (with the statistical caveats of the previous section writ large) is a population with discrete generations when the

response variable is normally taken to be the change in population density from one generation to the next, measured on a logarithmic scale ($r_t$). Fluctuation in $r_t$ can then be explained in terms of a variety of explanatory variables, some of which may be time-lagged, and/or be functions of population density. Although the identification of some influences as density dependent may provide information about likely regulatory factors, the most influential factors driving population *fluctuations* may contribute absolutely nothing to population *persistence*.

We have labored these two interpretations of the top-down/bottom-up debate because confusions between the two are common in the literature. Thus, the demonstration of a strong bottom-up *influence* (in our usage of the term) has often been used to argue against top-down *regulation* (again in our usage of the term). But this is chalk and cheese, a point forcibly made by George Varley over 20 years ago in his article on the control of the Bean Bug in Ruritania. Elements of both these debates are present in Hunter's article. The statistical techniques he uses, flawed though they may be, are consistent with partitioning variation in population fluctuations into top-down and bottom-up influences, as emphasized at the beginning of his abstract. But the beginning of the paper then emphasizes questions of regulation and limitation. Both debates are fascinating to ecologists, but mixing the two is a recipe for confusion. It is disturbing to find an article bearing Varley's name that muddies and confuses something he had thought so clearly about.

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