

HASSELL

SEEING THE WOOD FOR THE TREES: DETECTING DENSITY DEPENDENCE FROM EXISTING LIFE-TABLE STUDIES

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SUMMARY

(1) The analysis of sixty-three life-table studies involving fifty-eight insect species by Stiling (1988) is re-examined. In particular, we question his conclusion that the apparent absence of density-dependent processes in more than half of the studies meaningfully reflects the prevalence of such processes in natural systems.

(2) We show that the proportion of studies in which density dependence was detected by the original authors increases markedly with the number of generations available for analysis. This pattern is particularly clear from the twenty-eight life-tables available for univoltine insects.

(3) That density dependence was detected in a large proportion of the studies lasting for more than a few generations is an encouraging result considering the inadequacies in current methods for detecting the different types of density dependence that can act on insect populations.

INTRODUCTION

Most studies in which populations have been monitored over several generations show fluctuations in population size around some characteristic level of abundance, quite unlike unbounded population growth or any 'random walk' inevitably meandering to extinction. Clearly, some kind of negative feedback process, acting for at least some of the time on at least part of the population, must be involved in the dynamics of such populations (except in the very unlikely event that density-independent gain and loss terms happen to be in almost exact balance over the period). Identifying these feedback processes by teasing out the density-dependent signal from the environmental noise, and explaining just how they operate, is of fundamental importance to ecology. Only then can such practical applications as harvesting of renewable resources, epidemiology, conservation of species and pest control be properly addressed on a truly scientific basis.

All populations are, of course, subject to different mixtures of predictable density-dependent effects and unpredictable environmental noise. In some field studies, however, no density dependence appears to have been detected, and yet the populations seem to be fluctuating erratically around some long-term average level of abundance, with the fluctuations clearly restricted in amplitude (e.g. Dempster 1975). This has led some authors to see density dependence as a sporadic process that imposes an upper 'ceiling' and a lower 'floor' on the population fluctuations, leaving the populations free for the rest of the time to fluctuate erratically between these two levels (Milne 1957; Strong 1986; Stiling 1988). Most of these ideas have been framed in verbal terms. In essence, such a 'floor-and-ceiling' model ultimately represents no more or less than one sharply

discontinuous shape for the density-dependent regulatory processes. Sinclair (1989) has recently given an incisive review of the history of these ideas.

In an interesting recent study, Stiling (1988) has surveyed sixty-three published life-table studies of insects from forty-nine separate studies, and lists all factors identified as density-dependent or acting as a key factor. He found that 'density-dependent processes were not identified in 46.9% of the cases. In the remaining 53.1%, no one density-dependent process was of paramount importance in exerting "control" over the populations.' From these statistics he concluded that many insect populations are not regulated by density-dependent factors acting across the usual range of population densities.

It is outside the scope of the present paper to re-examine in detail these individual studies in an attempt to analyse the data uniformly. Indeed, it is still far from clear how density dependence is best detected from such long-term data sets (Gaston & Lawton 1987; Pollard, Lakhani & Rothery 1987). Instead, like Stiling, we accept the original authors' findings on whether or not density dependence was detected. However, when examined in relation to the duration of the studies, the same data set point clearly to a much greater prevalence of density-dependent processes than is implied by Stiling's analysis.

METHODS

Of the sixty-three life-table studies involving fifty-eight insect species examined by Stiling (1988) (his Table 1), fifty studies were examined for density dependence by the original authors. These are indicated in our Table 1 together with the additional information of the duration of the study in terms of completed generations and, in the case of multivoltine insects, the number of generations per year. Table 1 also indicates the statistical methods used to detect density dependence. Some authors have regressed a measure of mortality against density looking for a positive correlation ('single regression'), while others have used the method of Varley & Gradwell (1960, 1968) where density dependence is only accepted if the regression coefficient of $\log S$ against $\log N$ is significantly less than unity and that of $\log N$ against $\log S$ is significantly greater than unity ('double regression'). This is an unnecessarily harsh test, requiring that density dependence remains apparent when *all* sampling errors are assumed in turn to lie first in the estimates of N and then in those of S (Hassell 1980; Hassell, Southwood & Reader 1987; Southwood *et al.* 1989). In response to this, Bartlett's (1949) regression method has sometimes been used in which sampling errors are equally distributed between both axes. We have used the term 'Unclear' in Table 1 where there is insufficient information given in the original papers to attach any of the other labels.

These different methods of testing for density dependence appear with different frequency in Table 1. There is a tendency for the 'single' and 'double' regressions to be used somewhat more often in longer lasting studies and to show density dependence with a slightly greater frequency than in the studies falling into the 'Bartlett' or 'Unclear' categories. Having said that, the biases introduced in this way are slight and do not explain the marked trends discussed below (see Figs 1, 2).

Our analysis rests largely on a re-examination of the same sixty-three studies considered by Stiling. Inevitably, not all of these are strictly comparable. For instance, in at least five cases both spatial and temporal data have been combined in the same analysis of density dependence: *Euphydryas editha* studied at twenty-three sites over four generations; *Henosepilachna pustulosa* studied at eleven sites for three generations;

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Hypera postica studied at four sites for up to five generations; *Wiseana cervinata* studied at three sites for three generations; and, the most extreme case, *Fiorinia externa* studied at thirty sites for only one generation. The importance of spatial density dependence in the regulation of populations, and problems in its detection from temporal runs of life-table data, have been recently discussed (e.g. Hassell 1985, 1987; Dempster & Pollard 1986; Mountford 1988; Walde & Murdoch 1988). However, mixing the two kinds of data—spatial and temporal—to increase the number of points available for analysis is unsound and best avoided. All the same, we have retained them here in order to consider the same selection of studies discussed by Stiling. (We are aware of a further ten examples not listed in Table 1 (see Table 2), and have also repeated our analysis with these included (Fig. 2).)

RESULTS

Notwithstanding the heterogeneity in the data and in the type of analysis, there are striking and interesting patterns in the frequency that density dependence has been detected from the cases in Table 1. The single most important factor is simply the duration of the studies. This is made clear from Fig. 1a, showing how density dependence is more likely to be detected as the number of generations available for analysis increases. Thus, with the inclusion of all cases in Table 1, only 54% purport to show density dependence. (The slight difference in this figure from the value of 53.1% obtained by Stiling (1988) is due, we suspect, to *Philaenus spumarius* being mistakenly included in the 'not tested' category.) By progressively shedding from the analysis all studies of less than a given duration, commencing with that of *Fiorinia externa* which lasted for only one generation (see above), this value is significantly increased. For example, density dependence was detected in 60% of the fifteen studies of more than ten generations and 70% of the ten lasting for more than twelve generations.

The examples in Table 1 include both univoltine and multivoltine species. The way that multivoltine species have been included in this analysis needs some explanation. In the original studies, some authors included all generations in their analysis, while others only looked for density dependence from the comparable generation in successive years. Which is correct will depend on the system in question and whether the agent causing the density dependence operates mainly on one, or on all of the generations within the year. We have followed the original authors in this, except where it is unclear what was done, in which case we have assumed that the analysis included all generations. There are twenty-eight univoltine cases, fifteen of which (53.6%) show some form of density dependence. This is almost the same proportion obtained from the twenty-two studies on multivoltine species (54.5%), indicating that both contribute more-or-less equally to the overall figure of 54% of the fifty cases analysed in Table 1 that show density dependence.

Because of these different ways that multivoltine species are treated, an obvious next step is to repeat the analysis considering only the univoltine species in Table 1. The length of the study now has a more striking effect (Fig. 1b), and density dependence is detected in 80% of the studies lasting longer than 10 years.

Finally, we have repeated the analysis in Fig. 1b to include the ten additional examples listed in Table 2. As shown in Fig. 2, the same increasing frequency of detecting density dependence in longer lasting studies remains clear. Density dependence is now apparent in nearly 70% of all cases, rising rapidly to 100% from studies of longer than 14 years.

TABLE 1. Density-dependent sources of mortality in insect population studies. Data from Table 1 of Stiling (1988) with some additional information on the length of the studies and the method used by the original authors for detecting density dependence (single, double, multiple or Bartlett regression, or method unclear)

| Species | Density dependence | | Generations (numbers per year) | Method of analysis | Reference |
|-----------------------------------|--------------------|--------|--------------------------------|--------------------|--------------------------------|
| | Source | Stage | | | |
| Lepidoptera | | | | | |
| <i>Andraca bipunctata</i> | None | | 10 (4) | Single | Bannerjee 1979 |
| <i>Bupalus piniarius</i> | Pd Ds | Larva | 15 (1) | Single | Klomp 1966 |
| <i>Operophtera brumata</i> | Pred | Pupa | 13 (1) | Double | Varley, Gradwell, Hassell 1973 |
| <i>Operophtera brumata</i> | None | | 8 (1) | Unclear | Embree 1965 |
| <i>Wiseana cerninata</i> | Disp | Adult | 10 (1) | Single | Barlow, French, Pearson 1986 |
| <i>Epiphyas postvittaria</i> | Paras | Larva | 16 (3) | Bartlett | Danthanarayana 1983 |
| <i>Papilio xuthus</i> | Paras | Egg | 12 (4) | Double | Hirose et al. 1980 |
| <i>Papilio xuthus</i> | None | | 10 (4) | Single | Watanabe 1981 |
| <i>Leptidea sinapis</i> | — | — | 8 (1) | Multiple | Warren, Pollard & Bibby 1986 |
| <i>Colias alexandra</i> | None | | 5 (1) | Unclear | Hayes 1981 |
| <i>Ladoga camilla</i> | None | | 5 (1) | Not tested | Pollard 1979 |
| <i>Malacasoma neuustria</i> | Disp | Adult | 8 (1) | Single | Shiga 1979 |
| <i>Coleophora serratella</i> | — | — | 7 (1) | Unclear | LeRoux, Paradis & Hudson 1963 |
| <i>Spilnota ocellana</i> | — | — | 12 (1) | Unclear | MacLellan 1978 |
| <i>Archips argyrospilus</i> | — | — | 5 (1) | Unclear | LeRoux, Paradis & Hudson 1963 |
| <i>Ostrinia nubilalis</i> | — | — | 5 (1) | Unclear | LeRoux, Paradis & Hudson 1963 |
| <i>Hyphantria cunea</i> | Fec | Adult | 8 (2) | Single | Itô & Miyashita 1968 |
| <i>Tyria jacobaeae</i> | Sv Dp Fc | Lv A-A | 11 (1) | Single | Dempster 1982 |
| <i>Pieris rapae</i> | — | — | 18 (3) | Single | Harcourt 1966 |
| <i>Phatella maculipennis</i> | None | | 18 (4) | Unclear | Harcourt 1963 |
| <i>Choristoneura fumiferana</i> | Sv Dp Fc | Lv A A | 16 (1) | Single | Morris 1963 |
| <i>Choristoneura pinus</i> | — | — | 3 (1) | Unclear | Foltz, Knight & Allen 1972 |
| <i>Euphydryas editha</i> | None | | 14 (1) | Unclear | Ehrlich et al. 1975 |
| <i>Euphydryas editha</i> | Sv | Larva | 4 (1) | Unclear | White 1974 |
| <i>Rhyacionia frustrana</i> | Paras | Egg | 6 (3) | Single | Garguillo & Berisford 1983 |
| <i>Parnara guttata</i> | Paras | Egg | 5 (3) | Single | Nakasugi 1982 |
| <i>Anthocharis cardamines</i> | — | — | 3 (1) | Not tested | Courtney & Duggan 1983 |
| <i>Laspeyresia pomonella</i> | — | — | 12 (1) | Unclear | MacLellan 1977 |
| Homoptera | | | | | |
| <i>Saccharosydne saccharivora</i> | Paras | Nymph | 12 (6) | Double | Metcalfe 1972 |
| <i>Parlatoria oleae</i> | None | | 18 (2) | Unclear | Huffaker & Kennett 1966 |
| <i>Leptoterna dolabrata</i> | Fec | Adult | 7 (1) | Single | McNeil 1973 |
| <i>Erastus ocellaris</i> | None | | 12 (2) | Bartlett | Waloff & Thompson 1980 |
| <i>Psammotettix confinis</i> | None | | 5 (2) | Bartlett | Waloff & Thompson 1980 |
| <i>Dicranotropis hamata</i> | None | | 10 (2) | Bartlett | Waloff & Thompson 1980 |
| <i>Diplocolenus abdominalis</i> | None | | 6 (1) | Bartlett | Waloff & Thompson 1980 |
| <i>Elymana sulphurella</i> | None | | 6 (1) | Bartlett | Waloff & Thompson 1980 |
| <i>Deltocephalus coronifer</i> | None | | 6 (1) | Bartlett | Waloff & Thompson 1980 |
| <i>Aleurotrachelus jelinekii</i> | None | | 11 (1) | Double | Southwood & Reader 1976 |
| <i>Fiorinia externa</i> | Paras | Nymph | 1 (1) | Single | McClure 1977 |
| <i>Tsugaspidiotus tsugae</i> | — | — | 6 (2) | Unclear | McClure 1981 |
| <i>Fiorinia theae</i> | — | — | Several | Not tested | Munir & Sailer 1985 |
| <i>Cicadella viridis</i> | None | | 3 (1) | Not tested | Tay 1972 |
| <i>Stenocranus minutus</i> | None | | 2 (1) | Not tested | May 1971 |
| <i>Nephotettix cincticeps</i> | Fec | Adult | 24 (3) | Single | Kuno & Hokyo 1970 |
| <i>Nilaparvata lugens</i> | Disp | Adult | 24 (3) | Single | Kuno & Hokyo 1970 |
| <i>Philaenus spumarius</i> | Conglom | Adult | 7 (1) | Single | Whittaker 1973 |

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(Table 1 continued)

| Species | Density dependence | | Generations (numbers per year) | Method of analysis | Reference |
|----------------------------------|--------------------|-------|--------------------------------|--------------------|---------------------------|
| | Source | Stage | | | |
| Coleoptera | | | | | |
| <i>Phytodecta olivacea</i> | None | | 5 (1) | Unclear | Richards & Waloff 1961 |
| <i>Hypera postica</i> | Fungus | Larva | 5 (1) | Single | Harcourt & Guppy 1977 |
| <i>Leptinotarsa decemlineata</i> | Paras | Larva | 3 (2) | Unclear | Latheef & Harcourt 1974 |
| <i>Leptinotarsa decemlineata</i> | Mg Sv | A Lv | 6 (1) | Single | Harcourt 1971 |
| <i>Homocidus septentrionalis</i> | Disp Fc | A A | 3 (1) | Single | Nakamura & Ohgushi 1981 |
| <i>Stenobothrus ventralis</i> | None | | 8 (1) | Single | Berryman 1973 |
| <i>Stenobothrus inornata</i> | — | — | 4 (0.5-1) | Not tested | Grimble & Knight 1970 |
| Diptera | | | | | |
| <i>Erioschia brassicae</i> | Pred | Pupa | 9 (3) | Double | Benson 1973 |
| <i>Erioschia brassicae</i> | Host Dth | Pupa | 6 (2) | Single | Hughes & Mitchell 1960 |
| <i>Oscinella frit</i> | None | | 6 (2) | Unclear | Allen & Pienkowski 1975 |
| <i>Delia coarctata</i> | Disp | Adult | 11 (1) | Double | Kowalski & Benson 1978 |
| <i>Taxomyia taxi</i> | None | | 8 (0.5-1) | Single | Redfern & Cameron 1978 |
| Orthoptera | | | | | |
| <i>Zoniocerus variegatus</i> | — | — | 4 (1) | Not tested | Chapman, Page & Cook 1979 |
| <i>Chrotocetus</i> | None | | 8 (3) | Double | Farrow 1982 |
| <i>Chrotocetus</i> | | | | | |
| <i>Leptocercis dispar</i> | Paras Pd | Adult | 6 (1) | Bartlett | Sanchez & Liljestrom 1986 |
| Hymenoptera | | | | | |
| <i>Cyzenis albicans</i> | Pred | Pupa | 15 (1) | Double | Hassell 1969 |
| <i>Neodiprion setifer</i> | None | | 11 (1) | Single | Lyons 1977 |

Abbreviations as follows: —, not examined for density dependence; 'A', adult; 'Conglom', conglomerate; 'Disp' or 'Dp', dispersal; 'Ds', disease; 'Fec' or 'Fc', fecundity; 'Host dth', host death; 'Lv', larvae; 'Mg', migration; 'None', density dependence not found; 'Paras' or 'Ps', parasitism; 'Pd' or 'Pred', predation; 'Sv', starvation; 'Mg', Migration.

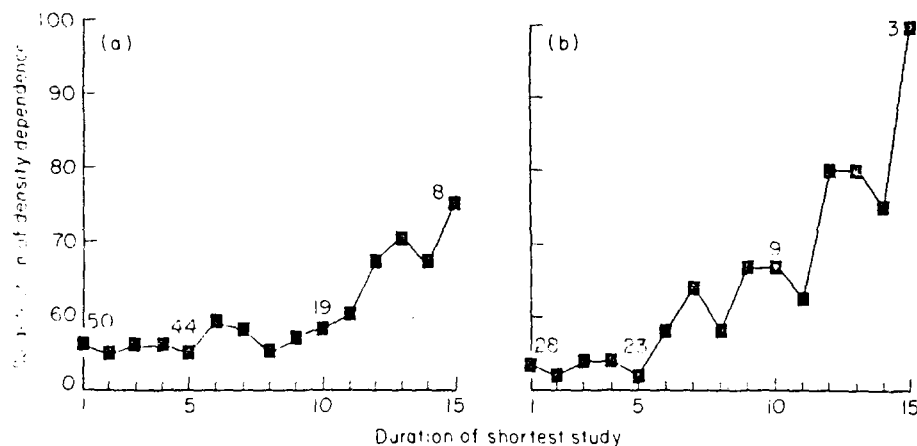


FIG. 1. The effect of the duration of the studies (in generations) on the probability of detecting density dependence. (a) Using the fifty examples in Table 1 that Stiling (1988) found were analysed for density dependence, and (b) using only those involving univoltine species. In both cases the relationship rises as studies of shorter duration than the abscissa values are shed from the analysis. The falling sample sizes of the first, fifth, tenth and fifteenth points are marked above each line.

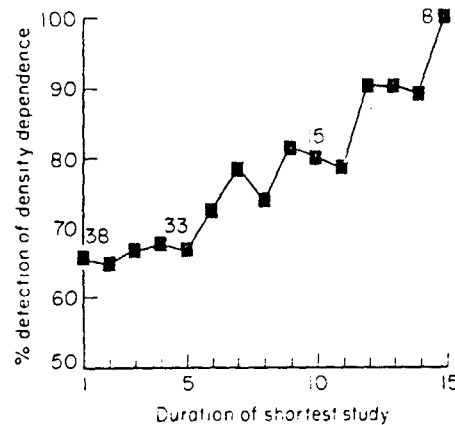


FIG. 2. As for Fig. 1b but also including the ten further cases in Table 2. Like Fig. 1, the frequency of detecting density dependence is greater in the studies lasting for longer periods.

TABLE 2. Additional studies (not given in Table 1) included in the analysis of density dependence shown in Fig. 2 (columns correspond to those in Table 1)

| Species | Density dependence | | Generations (numbers per year) | Regression method | Reference |
|------------------------------|--------------------|-------|--------------------------------|-------------------|------------------------------|
| | Source | Stage | | | |
| Lepidoptera | | | | | |
| <i>Pardia tripunctata</i> | Pred | Pupa | 7 (1) | Single | Bauer 1985 |
| <i>Notocelia roborana</i> | Pred | Pupa | 7 (1) | Single | Bauer 1985 |
| <i>Erranis leucophaeria</i> | Pred | Pupa | 15 (1) | Double | Ekanayake 1967 |
| <i>Erranis defoliaria</i> | Pred | Pupa | 15 (1) | Double | Ekanayake 1967 |
| <i>Erranis progemmaria</i> | Pred | Pupa | 15 (1) | Single | Ekanayake 1967 |
| <i>Erranis aurantiaria</i> | Pred | Pupa | 15 (1) | Single | Ekanayake 1967 |
| <i>Acleris variana</i> | Paras | Larva | 11 (1) | Single | Morris 1959 |
| <i>Zeraphera diniana</i> | Ds | Larva | 17 (1) | Single | Varley & Gradwell 1970 |
| Homoptera | | | | | |
| <i>Neophilaenus lineatus</i> | Paras | Adult | 6 (1) | Double | Whittaker 1971 |
| Diptera | | | | | |
| <i>Aedes aegypti</i> | ? | Larva | 9 (1) | Single | Southwood <i>et al.</i> 1972 |

CONCLUSIONS

Comparative surveys of the literature have proved very valuable in identifying general patterns in biology (e.g. Ridley 1983; Walde & Murdoch 1988; Pagel & Harvey 1989). Such surveys, however, can easily mislead without a sufficiently rigorous analysis (see Harvey & Mace 1982). Moreover, subtle biases in the data base or systematic trends in environmental parameters can undercut comparative surveys, no matter how well designed. There may, for instance, be a tendency for investigators to accumulate longer runs of data on populations that are steadier (which could result in density-dependent effects seeming to be more marked in populations that have been studied longer).

Stiling's (1988) survey of insect life-table studies (Table 1), found that density

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dependence—as detected by some form of regression analysis of mortality, fecundity, dispersal rates, etc. against density at a particular developmental stage—was only manifest in about half of the cases. Stiling suggests that the remaining half may be candidates for an alternative theory of population regulation, in which density dependence acts only occasionally to set a 'ceiling' and a 'floor' to population fluctuations, between which stochastic processes drive the pattern of population changes. We are critical of these views, for two main reasons. Firstly, on theoretical grounds, similar patterns of population behaviour—apparently erratic fluctuations between an upper and a lower limit—can arise deterministically as 'chaos', generated by a whole range of models for density-dependent population regulation (May 1974; May & Oster 1976; Gleick 1987). There is therefore no natural dichotomy between 'density-dependent regulation' and 'erratic fluctuations between a floor and ceiling' (May 1986). Secondly, on empirical grounds, we draw different conclusions from the data surveyed by Stiling.

Our analysis of the life-table studies in Table 1 suggests that density-dependent processes, operating over much of the observed range of population densities, were indeed detected in the great majority of studies in which adequate data for such tests were collected. In fact, density dependence was detected in almost all the studies that continued for more than a few generations. This is a most encouraging result, considering the inadequacies that may be present in some statistical and sampling techniques that are currently used for detecting the different types of density dependence that can act on insect populations (e.g. Hassell 1985, 1987; Pollard *et al.* 1987). These inadequacies are mainly of two kinds: (i) where the studies have not been planned to detect density dependence arising from the many heterogeneities operating on individuals within the population in a given generation (e.g. May & Hassell 1988; Walde & Murdoch 1988; Hassell & Anderson 1989), and (ii) where inappropriate statistical tests have been used (M.J. Crawley & D. Cox, unpublished).

In the face of such evidence, we see little need, at least for insects, to cast aside the familiar notion of populations persisting by virtue of density-dependent processes operating over a broad range of population densities. Having said that, populations can clearly be regulated by forms of density dependence that can be difficult to detect using conventional life-table means; for example, if there are pronounced time lags (Hassell 1985; Dempster & Pollard 1986), or if the density dependence is in response to within-generation heterogeneities and is obscured by variability acting upon the population (May 1986; Hassell 1987). Alternatively, the density dependence may only act intermittently as, for example, when caused by generalist predators whose feeding on a particularly prey is governed by such vagaries as alternative prey abundances. However caused, these are all manifestations of density-dependent population regulation, and the subject of population ecology would be well served if they were viewed within such a common framework rather than presented as alternative paradigms.

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