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Population dynamics of a tree-dwelling aphid: individuals to populations

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Abstract

The model presented simulates most of the observed features of the population dynamics of tree-dwelling aphids: a sharp increase in numbers during the first 15–40 days, followed by a sharp decline to a plateau of low numbers in summer and a recovery in autumn, in some years. The larger the numbers at the beginning of the season, the larger and earlier the peak. Migration is shown to be the most important factor determining the summer decline in abundance, while changes in aphid size and food quality account for why the autumnal increase is less steep than in spring. Finally, the model suggests a possibility of a “see-saw effect” (a negative correlation between spring and autumn peak numbers) in some cases.

Keywords: Insects; Oak aphid; Population dynamics; Seasonality

1. Introduction

The population dynamics of deciduous tree-dwelling aphids have been studied over long periods of time and in considerable detail. The regularity of the population fluctuations from year to year, very regular 2-year cycles and chaos, as indicated by suction trap catches, has proved very attractive to modellers, who have applied time series analysis to the data (e.g., Turchin, 1990; Turchin and Taylor, 1992). The 2-year cycles can be explained by the “see-saw effect”: a negative

correlation between the numbers of first generation aphids in spring (fundatrices) and the last generation in autumn (oviparae). This effect has been observed in some empirical data (Dixon, 1971), but in other species (our unpublished data) it is not present or very weak.

Within a year, the dynamics of these aphids are very complicated and in looking for the mechanism of regulation this needs to be taken into consideration. For example, in the case of the Turkey-oak aphid, *Myzocallis boerneri*, an initial dramatic increase in population size in spring is typically followed by a steep decline in abundance during summer and sometimes a further increase in autumn. During spring and summer all the generations are parthenogenetic, short

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lived (2–4 weeks) and fully winged. In autumn, sexuals are also produced, which mate and give rise to the overwintering eggs that hatch the following spring and give rise to fundatrices, the first parthenogenetic generation.

A lot is known about the biology of the parthenogenetic generations of aphids, in particular, the optimum behaviour for maximising the instantaneous population growth rate, r_m , under various environmental conditions (Kindlmann and Dixon, 1989, 1992; Kindlmann et al., 1992) and the optimal strategies for migration (Dixon et al., 1993a). Therefore, all the parameters needed to build a model to explain their population dynamics on the basis of their evolutionarily stable optimal behaviour are known. Such a model will not only describe, but also explain the patterns observed.

The parthenogenetic generations overlap in time and the environmental conditions are rapidly changing. Therefore, an individual throughout its life, as well as individuals born at different, but close instants in time, can experience quite different conditions, which results in them using different and varying reproductive strategies. Thus any model that lumps together the different age stages is inappropriate as an individual-based model is needed.

In this paper an individual-based model is presented which incorporates all that is known about the biology of tree-dwelling aphids. The predictions and conclusions are compared with an extensive data set on the population dynamics of the Turkey-oak aphid *Myzocallis boerneri*.

2. Material and methods

2.1. The larval development

The sizes of the soma and gonads of larvae and the size of the gonads and age of adults were monitored in a matrix, which contained one row for each individual. In each time step (0.01 day), different procedures were followed for larvae and adults:

The changes in the size of the gonads and soma of larvae were assumed to follow the Kindl-

mann and Dixon (1989) model:

$$\begin{aligned} \frac{ds}{dt} &= as^\alpha - Rg, & s(0) &= s_0 \\ \frac{dg}{dt} &= Rg, & g(0) &= g_0 \end{aligned} \quad (1)$$

where s and g are sizes of soma and gonads at time t , respectively, R is the constraint on the gonadal growth rate, a is the assimilation rate, $\alpha = 2/3$ is a constant (surface to volume ratio) and s_0 and g_0 are birth sizes of soma and gonads. The simulations of Eq. 1 were performed in 20 000 steps, simulating a season 200 days in length with time step equal to 0.01 day, using a difference method. At birth, the size of soma was assumed to be equal to 25 units, a unit corresponding to 1 μg for the species considered; this can be used for other species if the units are changed (i.e., if e.g. the birth size were 50 μg , then a unit 2 μg would have to be used). The size of gonads at birth was assumed to be that predicted by the optimisation process described in Kindlmann et al. (1992). The function

$$g_0 = (1 + 0.01s_0)a^2 \quad (2)$$

approximates the results of that optimisation fairly accurately and was used instead of repeating the lengthy optimisation. There exists, however, no analytical proof of this dependence.

The constraint on the gonadal growth rate, R , was assumed to be equal to 0.5 $\mu\text{g}/\mu\text{g}/\text{day}$, as this is the value common in aphids (Kindlmann and Dixon, 1992). The assimilation rate, a , was not constant, as in the original model, where the predictions were verified using results of laboratory experiments done under constant conditions. In the field, the assimilation rate changes dramatically during the course of the season and follows changes in the quality of the host plant. The concentration of total free amino acids in the leaves can be used as a good indicator of host quality and Dixon et al. (1993b) indicate a parabolic dependence of this quality on time. In addition to changes in host plant quality, the (negative) influence of cumulative aphid population density on host plant quality was also consid-

ered. Therefore, the equation

$$a(t) = \frac{((t - t_{\min})/t_{\min})^2 \cdot (A_{\max} - A_{\min}) + A_{\min}}{d/C + 1} \quad (3)$$

was used to estimate a , where d is the cumulative aphid population density (calculated from the model), C a scaling constant, A_{\max} the maximum value of a at the beginning of the season ($t = 0$), A_{\min} the minimum value of a at time t_{\min} (on an uninfested tree, i.e., $d = 0$ throughout the season).

If the season begins in April, the value $t_{\min} = 135$ is realistic for the time of minimum host plant quality, i.e., August. A change in the value of this parameter does not affect the qualitative

behaviour of the model and therefore $t_{\min} = 135$ was used in most of the simulations.

The values of A_{\max} , A_{\min} and C used in the simulations were varied over the range observed in aphids, e.g., $A_{\max} = 2.5$ was estimated from laboratory data (= good food quality) and its value is unlikely to differ much from this value (Kindlmann and Dixon, 1992). When food quality is poor, a has to be low. A good criterion for testing whether A_{\max} and A_{\min} are realistic, are the predicted sizes of the adults. If these were not realistic, the simulations were discontinued. The value of C was varied until the simulated population became extinct, or the model's output differed from that observed.

The simulations of Eq. 1 were stopped, when

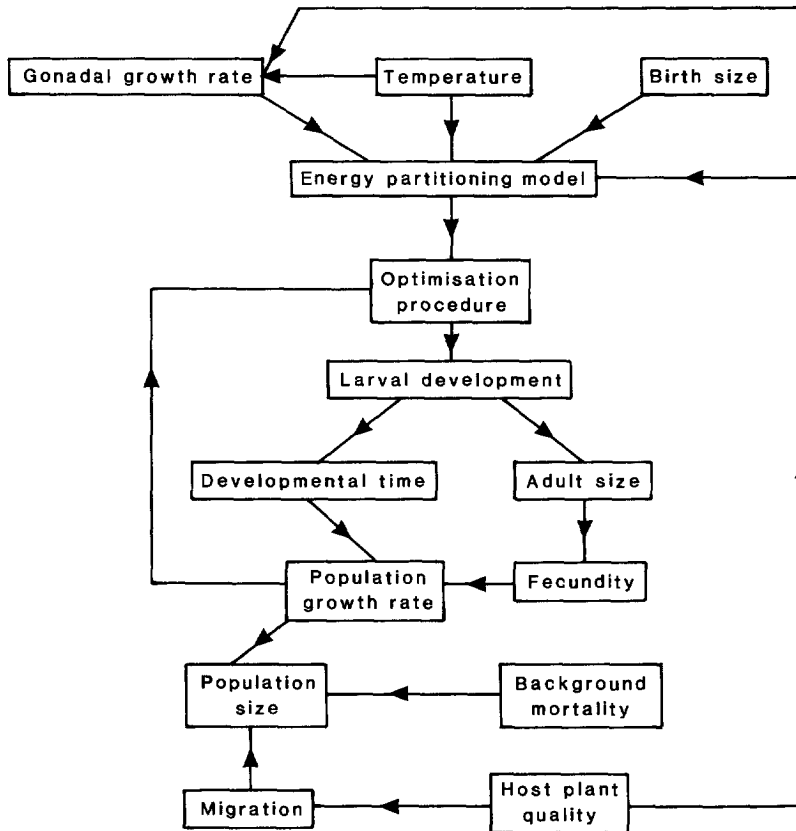


Fig. 1. The organisational diagram of the aphid model.

ds/dt became negative (at a time referred to as D , developmental time), i.e., when the animal became adult.

2.2. Adult life and reproduction

For adults, the relative size of the soma and gonads is irrelevant as only the size of the gonads at maturity, $g(D)$, determines fecundity. The shape of the reproduction curve (number of offspring born per mother per day), $F(t)$, was assumed to be positive only for $2D > t > D$ and triangular:

$$F(t) = 2Rg(D)/(s_0 + g_0)(2 - t/D), \quad (4)$$

where t is the age of the individual (Kindlmann et al., 1992). As only integer increments in the number of individuals can be simulated in the individual-based model, a step length 100 times longer than in the simulation of larval growth was used. Fractions of $F(t)$ were rounded randomly up or down with a probability determined by the value of the fraction. This is important especially when the values of a are low, animals are small

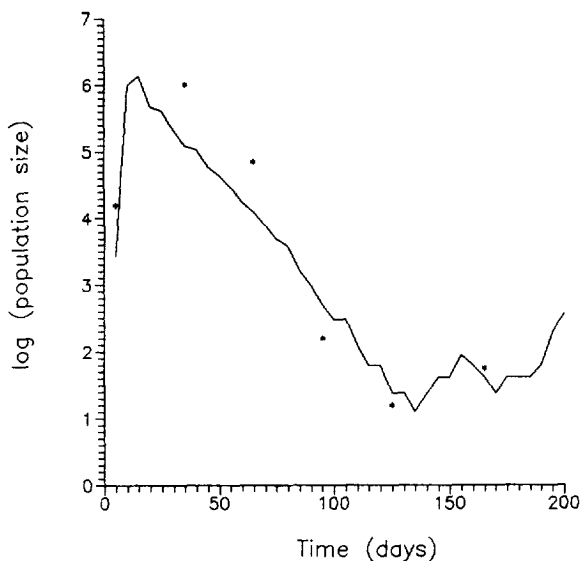


Fig. 2. The average seasonal pattern of density changes of *M. boernerii* populations on two Turkey-oak trees in Norwich, England, from 1975 to 1992 (*), fitted by the model (—). Parameters: $A_{\max} = 2.5$, $A_{\min} = 0.01$, $R = 0.5$, $s_0 = 25$, $t_{\min} = 135$, $S = 0.005$, $i = 0.1$, $C = 2 \cdot 10^6$. Log of initial number of aphids: 1.5.

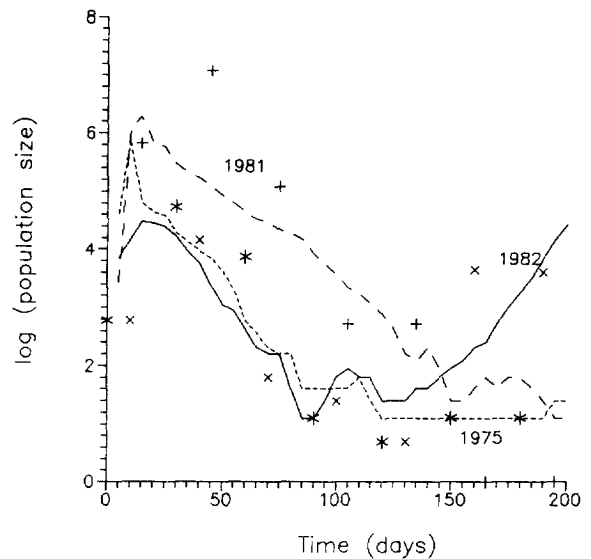


Fig. 3. Empirical data on density changes of *M. boernerii* for 1975 (*), 1981 (+) and 1982 (x) and simulation results showing the same trends. Parameters are the same as in Fig. 2, with the following exceptions: 1975, $S = 0.01$; 1981, $t_{\min} = 185$; 1982, $t_{\min} = 100$, $A_{\max} = 1$.

and fecundity is low. The procedure used corresponds with the empirical data: small adult aphids do not reproduce every day, producing a single larva at longer intervals.

The mortality due to predators, aphids falling from the leaves etc., was assumed to be constant. When this value was varied, it did not have any effect on the qualitative behaviour of the model and therefore only the outputs using a value of 0.15 for background mortality per iterative step are presented.

2.3. Migration

The proportion of aphids that fly away from a colony, m , was assumed to be a linear function of the number of aphids (larvae + adults) present in the colony, x , with positive slope S and positive intercept i (Barlow and Dixon, 1980), times a linear function depending on a :

$$m = \frac{(Sx + i) \cdot (A_{\max} - a)}{A_{\max} - A_{\min}}. \quad (5)$$

The second term in Eq. 5 simulates the reluctance of aphids to migrate, when living on a good

host plant, and their willingness when on a poor quality plant.

The success of an aphid in finding another host plant is assumed to be in the range of 0.01 (Taylor, 1977). Therefore, the immigration from other colonies was assumed to be equal to $0.01m$. For the same reason as cited for calculating fecundity, the time step used was 100 times longer than for larval development.

Because the output of the model was dependent on, e.g., fecundity being randomly rounded up and down, each simulation was repeated 10 times. The calculations were performed on an HP Apollo computer using FORTRAN language.

2.4. The empirical data

The temporal pattern of density fluctuations of *M. boernerii* populations on two Turkey-oak trees

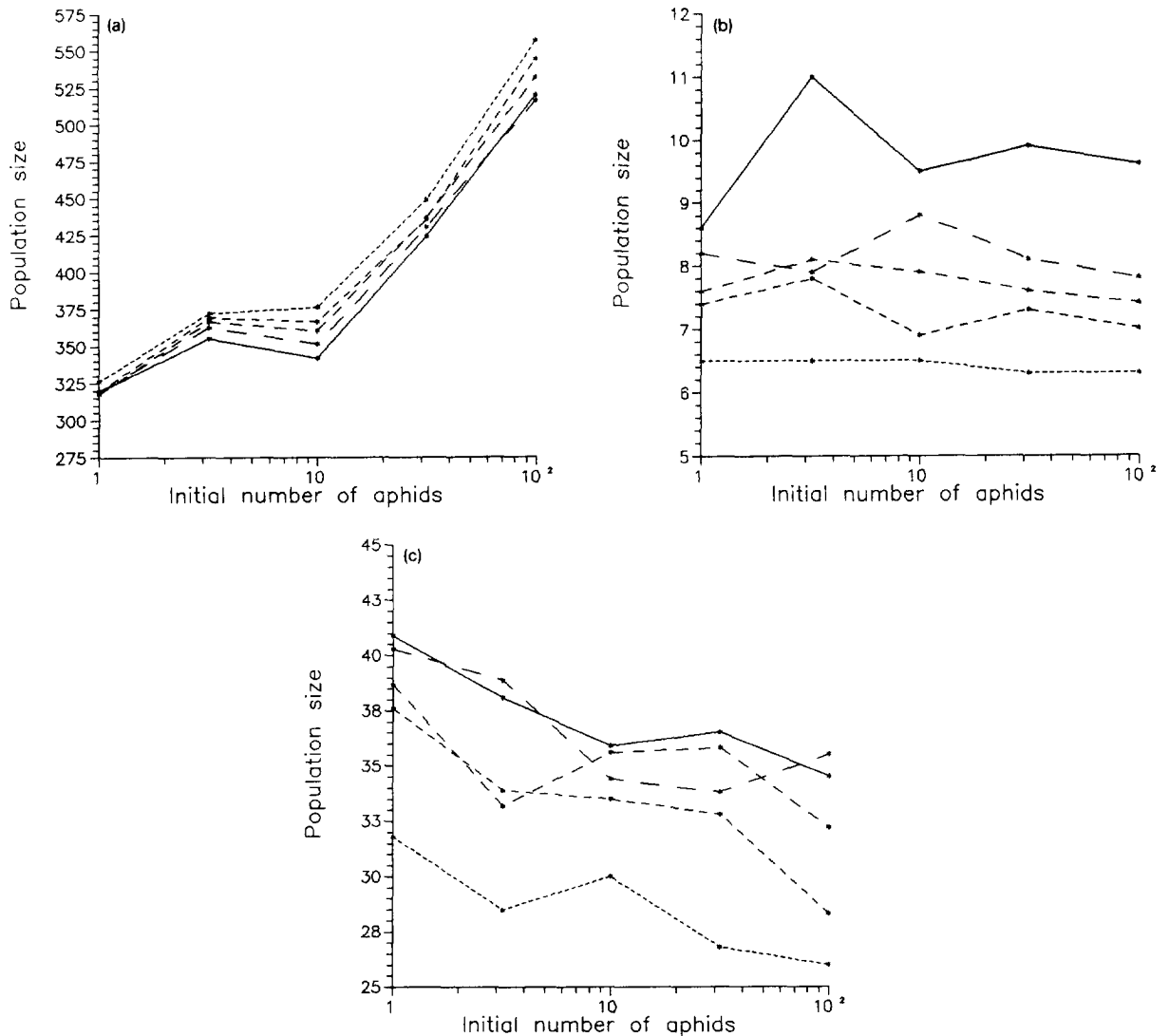


Fig. 4. Model predictions of the peak densities (a), the summer minimum densities (b) and of the final densities (c) plotted against the initial densities for $A_{\min} = 0.5$ (solid line), 0.4, ..., 0.1 (the smaller A_{\min} , the shorter the dashes). Parameters used: $A_{\max} = 2.5$, $R = 0.5$, $s_0 = 25$, $t_{\min} = 150$, $S = 0.005$, $i = 0.1$, $C = 5 \cdot 10^4$. Log of initial number of aphids: 2.

in Norwich, England, from 1975 to 1992, were used. The populations were sampled at weekly intervals from the beginning of May to the end of November each year. Each week, 10 leaves were selected at random at each of 8 fixed sampling points around the circumference of the trees and the numbers of the various life stages recorded.

3. Results

The organisational diagram of the model described in the previous section is shown in Fig. 1. Not all the simulation results are depicted. The common feature of almost all the simulations was the sharp increase in total numbers at first, followed by a decline and then another increase in abundance. The peak number was reached very early each year in all cases: during the first 15–40 days. The more or less broad trough in population numbers never preceded the instant when *a* was lowest and occurred some 15–30 days later.

The possibility of simplifying the model by deleting some of the parameters was explored by varying those that were not measured directly. All such simplifications resulted in the model deviating from reality.

For example, deletion of the second term in Eq. 5, i.e. omission of the assumption that the tendency of aphids to migrate depends not only on their own density, but also on host plant quality, did not change the “up-down-up” population profile, but resulted in the peaks being of nearly the same size for a wide range of initial conditions, irrespective of the values of the other parameters. As the empirical data show a significant positive correlation of the peak value with the initial density, the second term in Eq. 5 cannot be omitted.

The average seasonal pattern of density changes of the Turkey-oak aphid, from May to November, for the period 1975–1992, was fitted by the model in Fig. 2. From the same period, 1975–1992, three years with very different patterns of density changes were chosen and data plotted in Fig. 3: 1981 – a high spring peak followed by a monotonous decline, second peak not present; 1982 – both spring and autumn peaks relatively low and of the same size; 1975 – the spring peak followed by a decline and a long plateau in autumn. To show the model’s ability to mimic different types of aphid behaviour, parameters were chosen to simulate the dynamics in these years, but not fitted to the data, in Fig. 3.

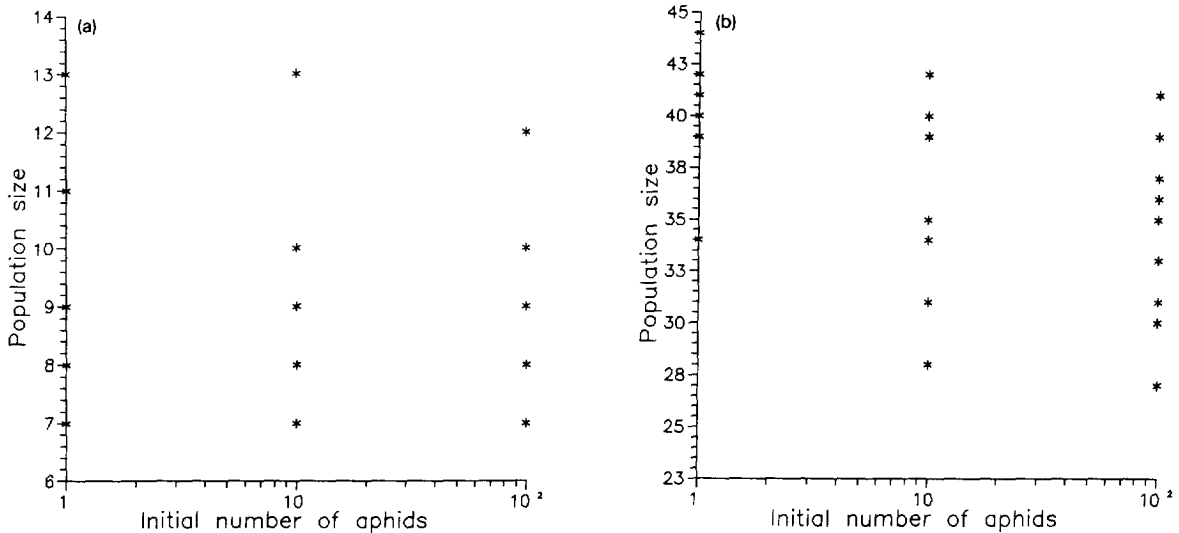


Fig. 5. Predictions of the final and minimum densities against the initial densities obtained from 10 runs of the model using different random numbers. $A_{\min} = 0.5$. Other parameters are the same as in Fig. 4.

A global view of the model's behaviour is given in Fig. 4, where the average peak densities, summer minimum densities and final densities obtained from 10 runs of the model are plotted against the initial densities for several values of A_{\min} . The peak densities are clearly dependent on the initial numbers but weakly so on the value of A_{\min} . Both the summer minimum and the final autumnal densities are dependent on A_{\min} ; the lower A_{\min} , the lower the corresponding density. They also decline when initial numbers and therefore also spring peak numbers (Fig. 4a) are increased (the "see-saw effect"), this being particularly so in the case of the final densities and negligible so for low A_{\min} and the minimum densities. Plotting the final and minimum densities against the initial densities obtained from 10 runs of the model reveals that the "see-saw effect" may be overshadowed by other phenomena (Fig. 5). Although the appropriate trend is there, variation due to random factors is very large.

As the empirical data indicates, the numbers of aphids present in summer are extremely low. This suggests that the actual values of C and A_{\min} are close to those used in the simulations illustrated in Figs. 2 and 3.

4. Discussion

The model satisfactorily describes the within-year population dynamics of the Turkey-oak aphid: a sharp increase in numbers in spring, which is usually followed by a sharp decline in summer and sometimes by a subsequent increase in autumn. The autumnal increase follows the improvement in food quality with a delay and is never so steep as in spring. The delay has a simple biological explanation: small summer individuals feeding on food of low, although rapidly improving quality, are not able to produce large offspring and their fecundity is also low. Therefore the effect of the autumnal improvement in food quality is reflected in the population dynamics but with a delay and the subsequent increase in numbers is less steep than for the large aphids living in the lush conditions prevailing in spring.

The model further reveals the regulatory

mechanism that is responsible for the summer decline in numbers: migration. This increases linearly with density and declines with improving food quality. The model outputs indicate that migration is important in shaping the population dynamics. If the decline were mainly due to low fecundity and high mortality, then the average realised number of surviving offspring per aphid would have to be – because of parthenogenesis – smaller than one! This seems unlikely, as even in the worst conditions the average reproductive output per aphid is about 1 offspring per 1–2 days and the reproductive life span is 10–20 days. Empirical data confirm that the tendency to migrate depends on density and food quality in the above mentioned way.

In the model, the extent of the summer decline in aphid abundance is determined by the degree to which the food quality declines in summer, which influences aphid size, fecundity, density and subsequently their tendency to migrate. Therefore, changes in food quality determine in this rather complicated way the changes in summer numbers. This prediction is rather difficult to test empirically and is a task for the future.

In contrast to most other groups, the empirical data do not lend support to a marked effect of natural enemies, or a severe scramble for resources by these aphids. Therefore, these factors do not seem to play a substantial role in regulating the abundance of these aphids. Food quality determines the rate of development and size of an individual more than intraspecific competition, and food quality is not affected by aphid numbers substantially (Dixon, 1971). Finally, a comparison of data presented here and by Dixon (1971) further supports the hypothesis that migration is responsible for the summer decline in numbers: while in nature there is no second increase in population numbers in the lime aphid, in glasshouse experiments there is (Dixon, 1971), which is possibly because the experiment was done in an enclosed space in which the probability of finding another host plant was greater than in the field.

The "see-saw effect", a negative correlation between the numbers of first generation aphids in spring (fundatrices) and the last generation in

autumn (oviparae), has been observed in some empirical data (Dixon, 1971), but in other species (our unpublished data) it is not present or very weak. The model presented here reveals, why this is the case: the “see-saw effect” is a statistical phenomenon, rather than a deterministic one. It is more likely to occur when the initial numbers and/or the summer population are very high and when the aphid has some, but not a large effect on the host plant.

If no cumulative density effect on aphid abundance is assumed in the model ($C = \infty$ in Eq. 3), it does not predict any “see-saw effect” (simulated, but not depicted). This is quite straightforward, as there is a lag of several generations between the summer and autumn peaks. Therefore there must be some “memory” in the system, which transfers information on abundance from spring to autumn. It is unclear what biological form this “memory” takes. A lag caused by predators is unlikely, as explained above. The cumulative density effect assumed in the model may be a consequence of either a persisting and therefore accumulating influence of the aphids on the plant, or of some carry-over effect between aphid generations. There is neither empirical evidence for the former, nor theoretical support for the latter.

Population census data are usually subject to a descriptive statistical analysis using a time series analysis approach, with the Turkey-oak aphid data used here being no exception (they were analysed, e.g., in Turchin, 1990; Turchin and Taylor, 1992). This paper analyses them from a different point of view: that based on a detailed knowledge of the biology of the group involved, aphids. This approach reveals the underlying mechanisms, rather than just describing the population trends. This model provides a good basis for a predictive

model. For this, however, more empirical data on the seasonal changes in food quality similar to those for sycamore (Dixon et al., 1993b) are needed along with a better understanding of the migratory behaviour of aphids.

Acknowledgements

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