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Density-dependent dispersal may explain the mid-season crash in some aphid populations

Alla Mashanova · Alan C. Gange · Vincent A. A. Jansen

Abstract Aphid population dynamics during the season show a characteristic pattern with rapid increase in numbers at the beginning followed by a sudden drop in the middle of the season. This pattern is usually associated with predation and/or change in food quality during the summer. By developing a mechanistic model of aphid population dynamics we show that this pattern can arise from density-dependent dispersal behaviour of aphids. The dynamics produced by the model were similar to those observed in real populations of the alder aphid (*Pterocallis alni*). The two mechanisms required for these oscillations to arise were the perception of density through the number of contacts with other individuals and the inter-generational transfer of information (the maternal effect). Both mechanisms are examples of delayed density-dependence and, therefore, this study adds to the evidence that delayed density-dependence might cause complex population dynamics. To reproduce the seasonal dynamics of the alder aphid with the model, the maternal effect was essential, indicating that this could be an important factor in alder aphid dynamics. According to our model, external regulations (e.g., predation and/or change in food quality) were not required to explain the highly oscillatory population dynamics of aphids during a season.

Keywords Emigration · Maternal effect ·
Mechanistic model · Oscillations · Population dynamics

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Introduction

Aphid population dynamics during the season have a characteristic pattern: a rapid increase in numbers at the beginning is followed by a sudden drop in the middle of the season (reviewed by Karley et al. 2004). This drop is often associated with population responses to increased predation or changes in plant quality (or both) which act via enhanced emigration, reduced fertility or increased mortality (Karley et al. 2004 and references therein). These authors concluded that the relative importance of these factors and mechanisms has yet to be established and that mathematical modelling offers a powerful addition to the empirical studies. Here, we use mathematical modelling to assess the effect of density in the form of density-dependent dispersal as a cause of the mid-season crash in aphid populations.

Dispersal involves three stages—emigration, a transient phase and immigration (Clobert et al. 2001; Bowler and Benton 2005). In this study, we concentrate on the first stage—emigration. Theoretical studies have shown that when population dynamics are affected by density, the particular form of the dispersal function (in particular the emigration rule) is important (Kindlmann and Dixon 1996; Johst and Brandl 1997; Ruxton and Rohani 1998; Ylikarjula et al. 2000; Hovestadt and Poethke 2006). Therefore, we carefully formulated several models to describe different density-dependent mechanisms for emigration and compared the output of these models to observations on alder aphid (*Pterocallis alni*) colonies.

The crucial part of the model lies in recognising that aphids (like other species) cannot census their density directly but they perceive it indirectly, for instance, through density-induced resource exploitation or through direct encounters with other individuals (Harrison 1980).

Dispersal in response to physical contacts with other aphids has been reported in a range of aphid species (Johnson 1965; Lees 1967; Toba et al. 1967; Sutherland 1969; Sutherland and Mittler 1971). The response to the number of contacts per se cannot be easily disentangled from the response to local density-induced reduction in food quality—Lees (1967) reported that, deprived of food, *Megoura viciae* became restless and consequently had more encounters which led to increased dispersal. In order to minimise effects of the decrease in host quality, we compared our model results with the empirical data for the alder aphid (*P. alni*), a tree-dwelling aphid, for which variation in host plant quality is unimportant (Gange 1995).

Another important factor affecting the perception of density is the maternal effect, defined as the transfer of information about past densities from mother to offspring (e.g., Benton et al. 2001; Fowler 2005). The role of the maternal effect in generating cycles is widely discussed with respect to small mammal populations (e.g., Inchausti and Ginzburg 1998), but it is also relevant for insects (Ginzburg and Taneyhill 1994). In aphids, crowding of mothers was shown to affect dispersal in *Megoura viciae* (Lees 1967), *Acyrthosiphon pisum* (Sutherland 1969), *Aphis fabae* (Shaw 1970), *Myzus persicae* (Sutherland and Mittler 1971), *Sitobion avenae* (Watt and Dixon 1981), and *P. alni* (Gange 1985). Kindlmann and Dixon (1996) suggested that some transfer of information between generations was needed to explain the "see-saw" effect in summer and autumn peaks in *Myzocallis boerneri*.

A possible cause of the maternal effect can be derived from the peculiar life history of aphids. In many aphid species, individuals can switch from being wingless to wing production with the proportion of winged morphs being a reliable measure of dispersal (Harrison 1980). Unlike many other insect species, during summer months aphids reproduce parthenogenetically (giving birth to live young) and so embryos (as well as embryos within embryos) are developing inside the mother's body and might be affected by the chemicals stimulating wing production. In species with both pre- and postnatal determination of wing production, the proportion of dispersers resulted from a combination of densities experienced by both mother and offspring [e.g., *A. fabae* (Shaw 1970), *S. avenae* (Watt and Dixon 1981) and *P. alni* (Gange 1985)] suggesting a cumulative effect of density on dispersal. The cumulative effect of density was used to explain the reduction of weight in adult lime aphids (Dixon 1998) and the rise and decline of aphid populations (Kindlmann et al. 2004).

The aim of this study was to test whether density-dependent dispersal can explain the decline in aphid numbers that typically takes place in mid-season. In the absence of external factors, we used a mechanistic model

of dispersal which assumes that individuals perceive their density through physical contacts with each other and that the information about density can be passed from mother to offspring. To address the role of the above assumptions in generating oscillations within the season, three models were compared—one in which dispersal depends directly on the density, one in which dispersal depends on the number of contacts an individual has had, and one in which the information on the number of contacts is passed over between mother and offspring.

Materials and methods

Population dynamics of alder aphid

The model was inspired by the alder aphid, *P. alni*, since alder trees provide a relatively constant food supply, whereas aphids feeding on herbaceous hosts are more likely to be affected strongly by the food quality of their host plant. We chose this species as an example for three reasons: (1) dispersers of *P. alni* are winged as opposed to wingless sedentary individuals, and therefore, it is easy to measure dispersal rate during the season, (2) unlike many other tree species, alder retain high quality leaves during the whole season (Dawson and Funk 1981; Gange 1995), which excludes the effect of seasonal changes in food quality, (3) the density-induced effect of alder aphid on the leaf condition is limited [even at the highest aphid density (400–500 aphids per leaf) the leaves showed no sign of wilting or any other damage; A. Mashanova, unpubl. data].

The above reasons make *P. alni* a convenient species to study density-dependent emigration (which is the first stage of dispersal). Another useful feature of *P. alni* biology is that immigration into colonised patches is negligible—when an aphid lands on a leaf which is already occupied it leaves straight away (Gange 1985). This allows us to model the population dynamics as a combination of just two processes—intrinsic population growth and density-dependent emigration.

Model description

Three mechanisms for density-dependent emigration were considered. In the simplest case, dispersal was made proportional to the density—the "direct response model". In the "behavioural response model", dispersal was made proportional to the number of contacts experienced by an individual, which resulted in a more complicated relationship between dispersal and density. Finally, the transfer of the information about the number of contacts between generations was added in the "maternal effect model".

We assumed a "contact" to be a physical contact between individuals. However, it can be any action by which an individual directly senses the presence of another individual. It can be argued that increased motility induced by the shortage of good feeding places might lead to an increased number of physical contacts (Lees 1967) and therefore, physical contacts might serve as a reliable indicator of other conditions as well as of density itself. Indeed, the effect of this "pseudo-crowding" on wing production in response to predators' presence was reported by Sloggett and Weisser (2004) and Kurnet et al. (2005). Similarly, a reduction in motility, for instance, through manipulation of the aphids by ants (Oliver et al. 2007) should lead to a decreased number of physical contacts.

The direct response model

In the simplest case, emigration is proportional to density and the model can be written as a logistic equation

$$\frac{dN}{dt} = N(r - kN) = rN\left(1 - \frac{k}{r}N\right) \quad (1)$$

where N is the population number, r is intrinsic growth rate, and k is per capita emigration rate (see Table 1 for a summary of all the parameters and variables). The initial number of individuals was fixed at ten for all the models.

The behavioural response model

When emigration is proportional to the number of contacts i experienced by an individual, the relationship between density and emigration need no longer be linear and can be modified by behavioural response at two stages—the rate of having a contact with another individual and the emigration rate defined by the number of contacts. This mechanism was implemented by dividing the population into i classes with $i = 0, 1, 2, 3\ldots$ where i is the number of contacts per individual. The rate with which new contacts

Table 1 The summary of the parameters and variables

Symbol	Definition	Units
r	Intrinsic growth rate (all models)	Time^{-1}
k	Per capita emigration rate (direct response)	Time^{-1}
c	Rate of having a contact with any particular individual (behavioural response and maternal effect)	Time^{-1}
α	Emigration rate in response to a single contact (behavioural response and maternal effect)	Time^{-1}
n_i	The number of individuals belonging to class i (which have had i contacts)	Individuals
N	Population size	Individuals
I	Expected number of contacts per individual	–

were made was assumed to be proportional to the population size N with the rate of having a contact with any particular individual c. The rate of emigration was assumed to be proportional to the number of contacts i and emigration rate in response to a single contact α. In biological terms, the latter describes the sensitivity to a single contact—for example, if $\alpha = 0.1$, ten contacts will be needed to produce the same effect as one contact with $\alpha = 1$. Defining the number of individuals in a class i as n_i, the dynamics of n_i (for $i \geq 1$) can be written as

$$\frac{dn_i}{dt} = cNn_{i-1} - cNn_i - \alpha i n_i \quad (2)$$

where $N = \sum_{i=0}^{\infty} n_i$ is the overall number of individuals. The first term in Eq. 2 represents the recruitment from the class with $i - 1$ contacts, the second term represents the loss due to transition to class $i + 1$ and the last term the loss due to emigration.

Assuming that new individuals were born into the class with zero contacts gave a separate equation for the class 0 dynamics

$$\frac{dn_0}{dt} = rN - cNn_0 \quad (3)$$

Initially, all individuals were placed in the n_0 class since in spring colonies of *P. alni* are founded by females hatching from eggs and having no previous contacts with other aphids.

By defining the average number of contacts per individual as

$$I = \sum_{i=1}^{\infty} i\frac{n_i}{N} \quad (4)$$

it is possible to write the dynamics of the population size N over time as

$$\frac{dN}{dt} = rN - \alpha\sum_{i=1}^{\infty} i n_i = rN\left(1 - \frac{\alpha}{r}I\right) \quad (5)$$

Note that the notations $\sum_{i=1}^{\infty} i\frac{n_i}{N}$ and $\sum_{i=0}^{\infty} i\frac{n_i}{N}$ are interchangeable since the term $i\frac{n_i}{N} = 0$ for $i = 0$. Then, by differentiating Eq. 4 with respect to time and using

$$\sum_{i=1}^{\infty} i n_{i-1} = \sum_{j=0}^{\infty} (j+1)n_j = \sum_{i=1}^{\infty} i n_i + N$$

the dynamics of I over time can be found as

$$\frac{dI}{dt} = c\sum_{i=1}^{\infty} i n_{i-1} - c\sum_{i=1}^{\infty} i n_i - \alpha\frac{\sum_{i=1}^{\infty} i^2 n_i}{N} - rI + \alpha I^2$$

$$= cN - rI - \alpha\left(\frac{\sum_{i=1}^{\infty} i^2 n_i}{N} - I^2\right) = cN - rI - \alpha \text{Var}I \quad (6)$$

where Var$I$ is the variance of I.

Since we have not found a satisfactory closure, we studied the behaviour of this model by using Eqs. 2 and 3 to run the numerical simulations in Mathematica 5.2. In our simulations we used as many classes as were required to ensure that the number of individuals in i_{max} class was no more than one individual (300 classes were enough to run the simulations used in Fig. 2).

The maternal effect model

During the summer months, aphids reproduce by giving birth to live young, and therefore, changes in mother's state can affect a developing embryo (Dixon 1998). It was assumed that instead of "making a decision" for an offspring to be winged or wingless, the parent simply passed on the information about the number of contacts it had experienced. We therefore placed newborn individuals into the same class to which their mothers belonged. Then, the dynamics n_i of a class i (for $i \geq 1$) became

$$\frac{dn_i}{dt} = rn_i + cNn_{i-1} - cNn_i - \alpha in_i \qquad (7)$$

with an equation for $i = 0$ being

$$\frac{dn_0}{dt} = rn_0 - cNn_0. \qquad (8)$$

Then, the dynamics of the total number of individuals N is given by Eq. 5 and the dynamics of I can be found following the same steps as used to obtain Eq. 6

$$\frac{dI}{dt} = c\sum_{i=1}^{\infty} in_{i-1} - c\sum_{i=1}^{\infty} in_i - \alpha \frac{\sum_{i=1}^{\infty} i^2 n_i}{N} + \alpha I^2$$

$$= cN - \alpha\left(\frac{\sum_{i=1}^{\infty} i^2 n_i}{N} - I^2\right) = cN - \alpha \mathrm{Var}I \qquad (9)$$

It can be shown that in this model I has a Poisson distribution when the distribution of contacts equilibrates (see the Appendix for details), which allows us to substitute the variance of I with its mean, thus closing the system:

$$\frac{dI}{dt} = cN - \alpha I \qquad (10)$$

The dynamics produced by this closed version of the model agreed well with the simulations run using Eqs. 7 and 8.

Equations 6 and 9 clearly show the difference between the maternal effect and the behavioural response models. In contrast to Eq. 6, the dynamics of I in the maternal effect model does not depend on the intrinsic growth rate r. This is because, in the maternal effect model, newborn individuals increase not only the number of individuals but also the total number of contacts registered in the population; therefore, the expected number of contacts per individual does not change. In contrast, in the behavioural response model, new individuals are "naïve" (with zero number of

contacts), and therefore, their birth reduces the expected number of contacts per individual.

Results

The long-term dynamics produced by the models are shown in Fig. 1. The direct response model (being a logistic equation) does not produce any oscillations—the approach to equilibrium $N^* = r/k$ is always monotonic. The behavioural response model, in principle, is able to produce small-amplitude oscillations for high values of contact rate c marking the region where transition from monotonic increase to monotonic decrease towards equilibrium occurs (Fig. 2a, b), but for a wide range of parameters, the dynamics of the population size produced by this model is monotonic. The equilibrium value of N can be approximated as

$$N^* \approx \frac{4\alpha r + 3\pi r^2 + \sqrt{3\pi}r^{3/2}\sqrt{8\alpha + 3\pi r}}{12\alpha c} \qquad (11)$$

(see the Appendix for the derivation). The maternal effect model can produce both monotonic and oscillatory approaches to equilibrium $N^* = r/c$. The oscillatory region is determined by the relationship between the dispersal rate in response to a single contact α and the intrinsic growth rate r. Oscillations were produced for $\alpha < 4r$ with the period of oscillations being

$$T = \frac{4\pi}{\sqrt{\alpha(4r - \alpha)}} \qquad (12)$$

(see the Appendix for the derivation).
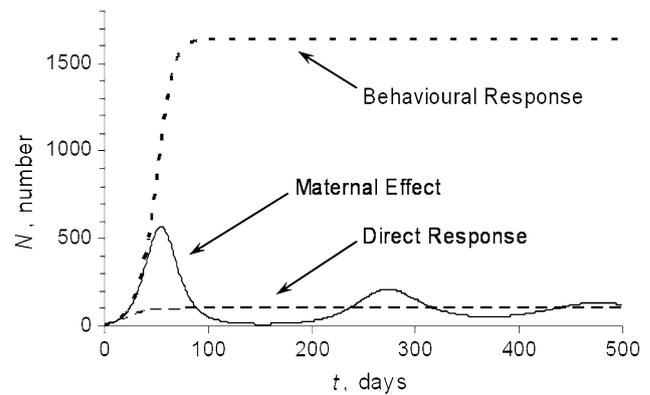
Fig. 1 The long-term population dynamics produced by the maternal effect (*solid line*), the behavioural response (*dotted line*) and the direct response (*dashed line*) models ($r = 0.1$, $k = c = 0.001$, $\alpha = 0.01$). The dynamics were obtained with Eq. 1 for the direct response model, Eqs. 2 and 3 for the behavioural response model, and Eqs. 5 and 10 for the maternal effect model. All dynamics started with ten individuals. Predicted equilibrium values are $N^* = r/k = 100$ for the direct response and the maternal effect models and $N^* \approx 1,637$ (Eq. 11) for the behavioural response model
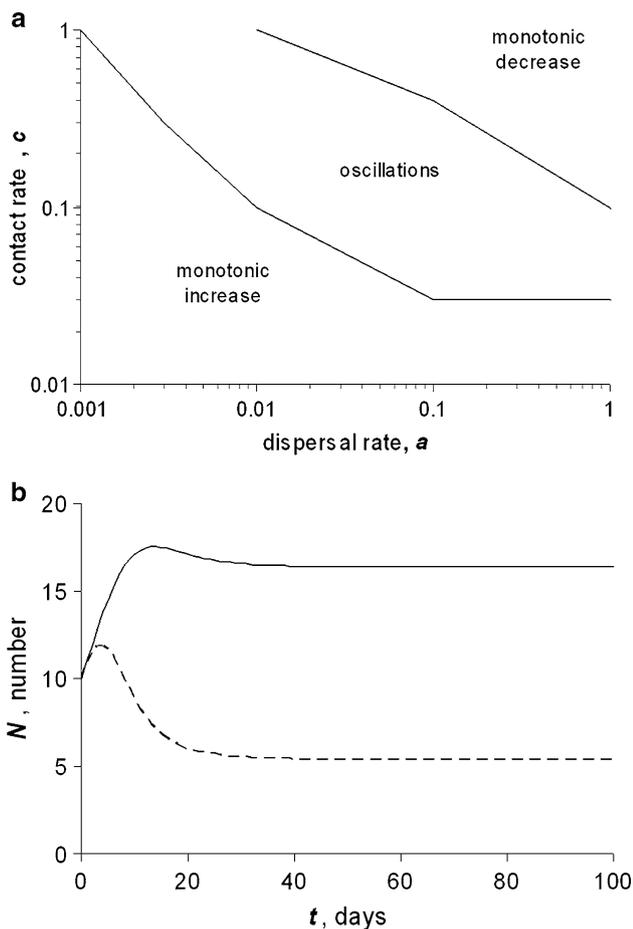
Fig. 2 **a** The parameter values for which oscillations are produced in the behavioural response model. The region of oscillations lies between the areas of monotonic increase and monotonic decrease towards equilibrium. **b** Two examples of population dynamics, $a = 0.01$, $c = 0.1$ (*solid line*) and $a = 0.005$, $c = 0.6$ (*dashed line*). All simulations were run using Eqs. 2 and 3 with intrinsic growth rate $r = 0.1$ and initial number of individuals ten

Comparison of the dynamics predicted by the behavioural response and the maternal effect models with the dynamics recorded for alder aphid

The behavioural response model and the maternal effect model were confronted with the dynamics of alder aphid described by Gange (1995) (Fig. 3a). We obtained the intrinsic growth rate r directly from the graph by observing that in late May-early June population growth of *P. alni* was approximately exponential, and r can be calculated from this part of the graph as being approximately 0.1. Further, we examined the oscillations in alder aphid's dynamics. In his study, Gange (1995) observed only one prominent oscillation during the reproductive season; therefore the length of the reproductive season (around 200 days) was used as the period of oscillations.

The combination of the above values for r and the period of oscillations allowed us to dismiss the behavioural
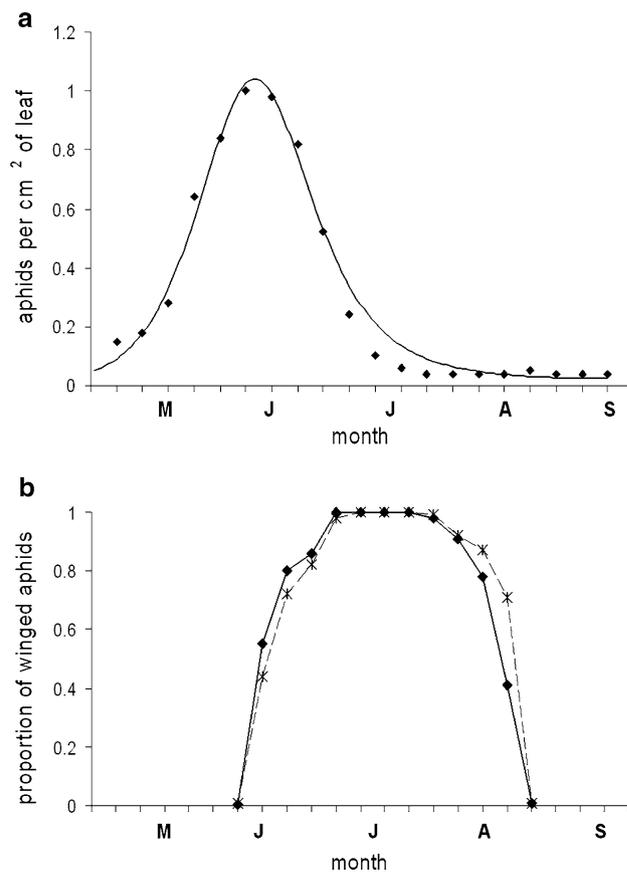
Fig. 3 **a** Seasonal dynamics (*diamonds*) of alder aphid *Pterocallis alni* (see Gange 1995 for details), and dynamics (*line*) produced by the maternal effect model (Eqs. 5 and 10, $r = 0.1$, $c = 0.0006$, $\alpha = 0.01$, $N_0 = 40$). Chosen values of r and α are explained in the text, c and N_0 were fitted to the aphid numbers [calculated as the values on the graph multiplied by 40 cm^2, which is the mean leaf area (Gange 1995)], using least-sum-of-squares method. **b** Two examples of the proportion of individuals developing wings in the fourth instar alder aphids (from Gange 1985)

response model: although this model is able to produce oscillations for the above value of r, the period of these oscillations was too short to match the observed value (Fig. 2b).

On the contrary, the maternal effect model is capable of producing oscillations with a wide range of periods including the observed $T = 200$ days. Using Eq. 12 and the observed values of T and r, the emigration rate α was calculated. For $T = 200$ and $r = 0.1$ there are two possible values for α in the maternal effect model: -0.01 and 0.39. The latter value lies close to the boundary of the oscillation region where the amplitude of the oscillation was negligible, and the dynamics resembled the monotonic approach to equilibrium. This left the maternal effect model with $\alpha = 0.01$ to be the only choice. The remaining contacts rate parameter c was fitted to minimise the sum of squares of residuals derived by subtracting model output from field

observations (Gange 1995). The dynamics produced by the maternal effect model with the above parameters matched the dynamics of alder aphid population well (Fig. 3a).

Our model suggests that the decrease in aphid numbers can be attributed to dispersal rather than other factors such as predation or increased mortality. If dispersal is indeed the main cause of the oscillation then it can be expected that the proportion of dispersers should increase with the decline in the population numbers during the season. Dispersers of alder aphids are easily distinguishable as they are winged (unlike wingless non-dispersers) and, therefore, this hypothesis can be tested. The population dynamics and wing production in alder aphid were studied by Gange in 1985. Early in the season during the fast growing phase of the colony growth there were very few winged aphids. Later during the season most of the developing aphids were winged, which coincided with a dramatic decline in numbers (Fig. 3b). This suggests that dispersal indeed plays an important role in the population dynamics of alder aphid.

Discussion

We have shown that the characteristic oscillatory dynamics of local aphid populations during the season can be explained by density-dependent dispersal without the need to invoke the influence of any external factors. Furthermore, the decline in the population numbers in the middle of the summer coincides with the increase in the proportion of winged individuals, suggesting that this decline could be attributed to dispersal rather than other processes, e.g., density-dependent mortality. Therefore, self-regulation (in a form of density-dependent emigration from local populations) could be responsible for the "mid-season crash" pattern even in the absence of seasonal changes in plant nutritional quality or natural enemy pressure, as suggested by Karley et al. (2004).

The three models, differing in the mechanisms underlying emigration of aphids, were tested. Our analysis differed from the traditional model-fitting in two ways. First, instead of fitting all the parameters of a model simultaneously (which often greatly improves a model's flexibility), we used the observed dynamics to obtain independent estimates wherever it was possible. Second, we excluded the models which produced dynamics that differed qualitatively from the observed dynamics. This allowed us to dismiss two models leaving only one—the maternal effect model—as an appropriate model. According to Burnham and Anderson (2002), this is an appropriate and important step in model selection, especially when the mechanisms are of interest. Our model study therefore leads to the conclusion that the maternal effect may play an essential role in the mid-season decline in aphid numbers. This finding is in accordance with other theoretical studies emphasising the importance of the maternal effect in regulating population dynamics (Benton et al. 2001; Fowler 2005).

The maternal effect model includes two behavioural mechanisms—perception of density through the number of contacts with other individuals and transfer of this information between generations. The first mechanism is shared with the behavioural response model but on its own is not enough to simulate characteristic aphid population dynamics (at least for the fast growing population of alder aphids). Without the maternal effect, population would reach much higher numbers, which potentially could lead to overexploitation of the resource. On the other hand, compared to the direct response model (where the response is proportionate to the actual population number), perception of density through the number of contacts results in higher population numbers lasting a limited time period. Therefore, the combination of these two mechanisms might serve as a fine regulation between under- and overexploitation of the available resource.

We used alder aphid as our case study organism because for this species the host quality does not vary significantly during the season (Dawson and Funk 1981; Gange 1995). Many other species of aphids (especially species with herbaceous hosts) experience dramatic changes in food quality which happen at a rate faster than density-dependent regulations. Consequently, even when present, these density-dependent regulations are likely to be overridden. Nevertheless, the presence of the maternal effect might serve as an indicator of density-dependent regulations even when the latter are hard to detect due to external regulations such as change in food quality or predation.

While dispersal in response to physical contacts in aphids has been confirmed in empirical studies (Lees 1967; Toba et al. 1967; Sutherland 1969; Sutherland and Mittler 1971; Gange 1985) we are not aware of any aphid population dynamics models incorporating this mechanism explicitly [but see Kindlmann and Dixon (1996) and Kindlmann et al. (2004) for models with dispersal being a linear function of, respectively, density and cumulative density]. If an individual "knows" the density, the response is instant and the dynamics are logistic ("direct response model"), but when the perception of density is mediated by the number of contacts with other individuals, a delay is introduced between a change in density and the dispersal response, which allows the population numbers to build up before falling (May 1973). Turchin (1990) pointed out that when density-dependent regulations are delayed, the effect of density on population dynamics is harder to detect. This difficulty might be responsible for the ongoing debate

about the role of density-dependence in population dynamics of aphids (Muller et al. 2001).

In many aphid species there is one rise and decline in numbers during the season (Sluss 1967; Gange 1995; Sequeira and Dixon 1997). The maternal effect model predicts a series of damped oscillations in the long run. A potential reason that such dynamics are not observed in field studies is due to the change from parthenogenetic to sexual reproduction in autumn followed by egg deposition, so that each season starts with a few individuals having no knowledge about the previous season. In such cases, the season is too short for multiple oscillations to appear. This provides a way to test our predictions experimentally. If delayed density-dependence indeed explains aphid population dynamics, multiple oscillations followed by stable equilibrium might be expected in less changeable conditions—for example, in laboratory populations on a relatively long-lived host. However, a potential problem arises from a rather low trough following the initial oscillation which hints that the population will only recover in a small number of runs (confirmed by running a stochastic equivalent of the maternal effect model).

Overall, this study showed that density-dependent dispersal on its own is able to cause characteristic mid-season crash dynamics. Although there is no doubt that in the real world it works in an interplay with other factors, it can be concluded that density-dependent dispersal might have a more profound effect on aphid population dynamics than was previously thought.

Appendix

Moment closure for the maternal effect model

The maternal effect model is defined by Eqs. 7 and 8. From Eq. 8, we obtain that, at equilibrium, $N^* = r/c$. By solving Eq. 7 for $dn_i/dt = 0$ and substituting the above equality for N^* we can calculate the equilibrium value n_i^* for the number of individuals in class i

$$n_i^* = \frac{cN}{cN - r + \alpha i} n_{i-1}^* = \frac{r}{\alpha i} n_{i-1}^* = \left(\frac{r}{\alpha}\right)^i \frac{1}{i!} n_0^* \tag{13}$$

Then, the overall number of individuals N^* is

$$N^* = \sum_{i=0}^{\infty} n_i^* = n_0^* \left(1 + \frac{\frac{r}{\alpha}}{1!} + \frac{\left(\frac{r}{\alpha}\right)^2}{2!} + \cdots\right) = n_0^* e^{\frac{r}{\alpha}} \tag{14}$$

from which $n_0^* = N^* e^{-\frac{r}{\alpha}}$ giving the probability mass function

$$p(i) = \frac{n_i^*}{N^*} = \frac{\left(\frac{r}{\alpha}\right)^i}{i!} e^{-\frac{r}{\alpha}} \tag{15}$$

which is the Poisson distribution.

Equilibrium population size for the behavioural response model

From Eq. 2, the equilibrium value for the number of individuals in class i is

$$n_i^* = \left(\frac{cN^*}{\alpha}\right)^i \frac{\Gamma\left(\frac{cN^*}{\alpha} + 1\right)}{\Gamma\left(\frac{cN^*}{\alpha} + 1 + i\right)} n_0^* \tag{16}$$

where $\Gamma(x)$ is gamma function. Summing over n_i^* gives the equilibrium population size

$$N^* = \sum_{i=0}^{\infty} n_i^*$$
$$= e^{\frac{cN^*}{\alpha}} \left(\frac{cN^*}{\alpha}\right)^{-\frac{cN^*}{\alpha}} \frac{cN^*}{\alpha} \left(\Gamma\left(\frac{cN^*}{\alpha}\right) - \Gamma\left(\frac{cN^*}{\alpha}, \frac{cN^*}{\alpha}\right)\right) n_0^* \tag{17}$$

where $\Gamma(x, x)$ is the incomplete gamma function. Equation 17 can be written as

$$N^* = e^z z^{1-z} (\Gamma(z) - \Gamma(z, z)) n_0^* \tag{18}$$

with $z = cN^*/\alpha$. Using Stirling's formula

$$\Gamma(z) \approx \sqrt{2\pi} z^{z-\frac{1}{2}} e^{-z}$$

and

$$\Gamma(z, z) = \frac{\Gamma(z + 1, z)}{z} - e^{-z} z^{z-1} \approx e^{-z} z^{z-1} \left(\sqrt{z\frac{\pi}{2}} - \frac{1}{3}\right)$$

(Abramowitz and Stegun 1965), Eq. 18 can be simplified to

$$N^* \approx \frac{1}{6} \left(2 + 3\sqrt{2\pi}\sqrt{z}\right) n_0^*. \tag{19}$$

Substituting z and $n_0^* = r/c$ (from Eq. 3) and solving Eq. 19 with respect to N^* gives

$$N^* \approx r \frac{4a + 3\pi r + \sqrt{3\pi r}\sqrt{8a + 3\pi r}}{12ac}$$

Local stability analysis for the maternal effect model

For the maternal effect model, the non-zero equilibrium values are $I^* = \frac{r}{\alpha}, N^* = \frac{r}{c}$. Following the standard local linearisation procedure, the stability of the system is defined by the Jacobian matrix

$$J = \begin{bmatrix} 0 & -\alpha\frac{r}{c} \\ c & -\alpha \end{bmatrix}$$

from which the eigenvalues are

$$\lambda = \frac{-\alpha \pm \sqrt{\alpha^2 - 4r\alpha}}{2}.$$

Oscillations arise when the eigenvalues have an imaginary part, which is when the expression under the square root is negative (i.e., if $\alpha < 4r$).

Since there are two eigenvalues, the general solution to the deviation of N from equilibrium has the form

$$n(t) = C_1 e^{\lambda_1 t} + C_2 e^{\lambda_2 t} \qquad (20)$$

(Gurney and Nisbet 1998). Defining $\omega \equiv \sqrt{4r\alpha - \alpha^2}$ and $i \equiv \sqrt{-1}$, we can write Eq. 20 as

$$n(t) = C_1 e^{\left(-\frac{\alpha}{2} + \frac{i\omega}{2}\right)t} + C_2 e^{\left(-\frac{\alpha}{2} - \frac{i\omega}{2}\right)t}$$
$$= e^{-\frac{\alpha}{2}t}\left(C_1\left(\cos\frac{\omega t}{2} + i\sin\frac{\omega t}{2}\right) + C_2\left(\cos\frac{\omega t}{2} - i\sin\frac{\omega t}{2}\right)\right)$$

and the period T can be calculated from $2\pi = \frac{\omega}{2}T$ giving

$$T = \frac{4\pi}{\sqrt{4r\alpha - \alpha^2}}$$

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