Evolution of cannibalism and female's response to oviposition-deterring pheromone in aphidophagous predators

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Summary

1. Egg cannibalism by larvae is common in Coccinellidae and is known to be advantageous for the cannibals. Furthermore, larvae of aphidophagous ladybirds usually produce an oviposition-deterring pheromone (ODP), which inhibits oviposition by adult females. It has been proposed that the response to ODP has evolved because of the high costs of cannibalism. However, this has never been formally proved.

2. In this paper, we study the theoretical evolution of this system. We first look at the conditions under which cannibalism and the response to ODP can evolve. Subsequently, we examine the occurrence of polymorphism both in the production of larval tracks and in the sensitivity of females to specific pheromones.

3. The models predict that the amount of cannibalism should not depend on prey density and that evolution should lead to a continuous increase in cannibalism, and consequently larvae should always cannibalize eggs when possible. In response to the cost of cannibalism, ODP recognition can evolve, so that females avoid laying eggs in patches of prey already occupied by conspecific larvae. The result is an arms race between larvae and adult females, which favours a diversification of ODP pheromones. Our models show that: (i) females should be able to recognize mixtures of hydrocarbons rather than a single molecule; and (ii) females should be more sensitive to the tracks of their own offspring than those of non-related larvae.

Key-words: egg cannibalism, evolution, ladybirds, modelling, oviposition-deterring pheromone

Introduction

For non-social Arthropods that do not provide parental care to their offspring, the survival of larvae is strongly dependent on the quality of the oviposition sites selected by gravid females. Since larvae usually have low dispersal capacity, it is unlikely they will be able to find a better place if they hatch in a poor quality site. The choice of oviposition sites is therefore crucial and has a large effect on the fitness of females (Resetarits 1996). Many insect species, whose food supplies are temporally limited, avoid the risk of competition between conspecific offspring by marking the resource (Gabel & Thiery 1992; Ruzicka 1996, 1997; Dempster 1997; Ruzicka & Havelka 1998; Anbutsu & Togashi 2001; Addesso *et al.* 2007; Liu, Yu & Li 2008). For instance, parasitoids avoid superparasitism by probing potential hosts (Agboka *et al.* 2002; Yamada & Ikawa 2005) or marking them with pheromones, which facilitates the detection of conspecifics within a host

(Vandijken, Vanstratum & Vanalphen 1992; Visser *et al.* 1992; Gauthier, Monge & Huignard 1996; Field & Keller 1999; Santolamazza-Carbone, Rodriguez-Illamola & Rivera 2004). With the exception of cases where larvae forage to find a host (Fournet *et al.* 2001), the females usually mark the hosts that they have just parasitized.

Aphidophagous predators face the same problems as parasitoids. This is particularly well studied in the case of ladybird beetles. Resources are regularly limited at particular periods of time, due to the ephemeral nature of aphid colonies (Dixon 1998). Whereas larvae need 4–5 weeks to develop, aphid colonies only last for 6–8 weeks and are thus a short-lived resource. For ladybirds, colonies of aphids are only suitable as oviposition sites during the 'egg window' (Dixon 2000). This window opens when a minimum critical density of aphids is reached (Dixon 1959; Honek 1980). Below this threshold, aphids are so rare that larvae have a low probability of catching their first prey and are therefore likely to die from starvation. Another risk of starvation occurs if the abundance of aphids in the patch declines before

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larvae complete their development. Thus, each colony supports an optimal number of eggs, which predators should not exceed even though the numbers of aphids are still increasing (Kindlmann & Dixon 1993). Females stop laying additional eggs when they discover tracks of conspecific larvae (Doumbia, Hemptinne & Dixon 1998; Yasuda, Takagi & Kogi 2000). After searching occupied patches and determining that they are unsuitable for oviposition, females eat some aphids and fly away (Frechette *et al.* 2004). Because of this adaptation to the ephemeral nature of their prey, the individual aggregative response of ladybirds to aphid density can be strong, but their numerical response is weak or restricted to a narrow range of aphid densities (Hemptinne, Dixon & Coffin 1992; Ives, Kareiva & Perry 1993).

Empirical evidence suggests that the evaluation of egg windows by adult females could be a response to the occurrence of egg cannibalism by larvae. Cannibalism has a great effect on the survival of eggs and young larvae in Coccinellidae (Osawa 1992; Yasuda & Shinya 1997; Snyder *et al.* 2000; Pervez, Gupta & Omkar 2006) and is commonly observed both under laboratory conditions and in the field (e.g. Osawa 1989; Hironori & Katsuhiro 1997; Schellhorn & Andow 1999). It is also strongly density dependent (Mills 1982).

At this point, it is important to differentiate the consequences of sibling cannibalism from those of non-sibling cannibalism. Sibling cannibalism can in theory be advantageous both for larvae and their mothers. When it occurs within the same egg batch, it provides the first meal for the larvae and contributes to a faster increase in body mass (Omkar, Pervez & Gupta 2007) and reduction in the duration of the first larval stage (Michaud & Grant 2004). As after dispersing from the eggs larvae can suffer from starvation, egg cannibalism increases their survival and their searching time for aphids (Majerus 1994).

Non-sibling cannibalism incurs a fitness cost for females. Therefore, we expect that strategies that mitigate the risk of non-sibling cannibalism have been selected for. For example, the two-spot ladybird *Adalia bipunctata* (L.) refrains from laying eggs on plants infested by aphids but contaminated by conspecific larval tracks (Doumbia *et al.* 1998; Frechette *et al.* 2004). They are deterred by the presence of an oviposition-deterring pheromone (ODP) deposited on the plant by the anal disc of the larvae (Laubertie *et al.* 2006). This ODP is a mixture of long aliphatic molecules, mainly alkanes (Hemptinne *et al.* 2001; Magro *et al.* 2007). Field observations indicate that aphidophagous ladybirds start laying eggs in aphid colonies quite early in the colony development and cease laying eggs as soon as colonies are marked by foraging first instar larvae. That is, the presence of ODP closes the egg window (Doumbia *et al.* 1998; Hemptinne *et al.* 2001). As the recognition of and reaction to ODP are a good means of preventing non-sibling egg cannibalism, many ladybird species developed this system. Although ODPs are commonly produced by insects dependent on ephemeral resources (Nufio & Papaj 2001), they are usually direct signals, i.e. the foraging females mark the resource and eventually use this information on a later visit to avoid a second exploitation (Godfray

1994). In the Coccinellidae, however, it is an indirect system. Larvae produce the ODP and this signal is detected by females. Whereas the importance of this marking pheromone for females is easily understood, the advantage for larvae is less clear.

Ladybirds always have interested theoretical biologists, who have been mostly concerned with their use as pest biocontrol agents (Dixon, Hemptinne & Kindlmann 1997; Dostalkova, Kindlmann & Dixon 2002). However, evolutionary studies on their life histories are rare (Kindlmann & Dixon 1999; Dixon & Hemptinne 2001). Furthermore, theoretical studies on oviposition strategies mainly focus on parasitoids. The main questions addressed are the duration of foraging bouts in patches, or the time at which females should start to super-parasitize, in relation to resource availability or competition. Aphidophagous predators differ from parasitoids in the occurrence of cannibalism, in that the larvae have to find and catch their prey, and in that they produce the signal that is used by foraging females to assess the quality of oviposition sites. In this paper, we study the evolution of ODP in aphidophagous predators by means of an evolutionary invasion analysis, which evaluated the selective advantage of mutants with different preferences for egg cannibalism or sensitivity to ODP. In the last part, we numerically investigate the occurrence of polymorphism in ODP produced by larvae and its recognition by females.

Description of the models

MODELLING STRATEGY

We model the population dynamics of aphidophagous ladybirds and their resource, the aphids, with an age-structured system of differential equations. For reasons of tractability, we neglect seasonal dependence of ladybird–aphid dynamics and use a continuous-time model. We first consider the dynamics of ladybird–aphid populations in the absence of cannibalism. Then, we consider the effects of cannibalism and the conditions for this behaviour to evolve. Subsequently, we consider the evolution of ODP synthesized by larvae. Finally, we study the effects of diversity in the composition of the ODP.

No-cannibalism model

The structure of this model is illustrated in Fig. 1. We assume three life-cycle stages for the ladybirds: eggs, larvae and adults, and only one stage for the aphids. The density at time t for each class is x, y, z and r respectively. The parameters used in the models are listed in Table 1. The equation for the change in egg density is given by:

$$\frac{dx}{dt} = \beta \cdot \eta \cdot r \cdot z - \lambda \cdot x - m \cdot x, \qquad \text{eqn 1}$$

where $\beta \cdot \eta \cdot r \cdot z$ denotes the production of eggs by adults, depending on the number of aphids they eat. λ and m refer to the death and maturation rates respectively. Changes in the density of larvae are given by:
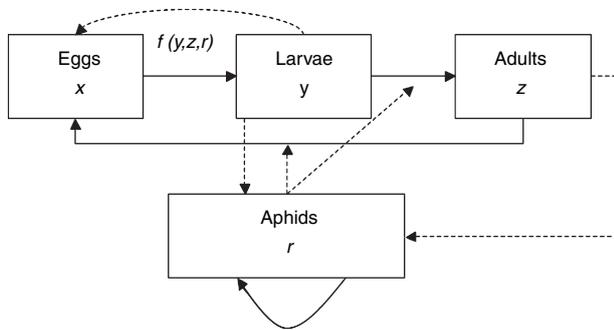
Fig. 1. Schematic diagram of the stage structure used in the models. The letters in each box represent the name of the corresponding state variable. $f(y,z,r)$ refers to the cannibalism function. In the first model, we assume the absence of cannibalism, so $f(y,z,r) = 0$.

Table 1. Model parameters with their descriptions

Scaled parameters	Description	In terms of original parameters	Value
β	Conversion rate (aphids to eggs) for adults	β	5
η	Predation rate of larvae	$\frac{\eta k}{\alpha}$	1
μ	Predation rate of larvae	$\frac{\mu k}{\alpha}$	1
m	Maturation rate of eggs	$\frac{m}{\alpha}$	1
γ	Conversion rate of larvae	γ	5
λ	Death rate of eggs	$\frac{\lambda}{\alpha}$	1
ξ	Death rate of larvae	$\frac{\xi}{\alpha}$	1
φ	Death rate of adults	$\frac{\varphi}{\alpha}$	1
α	Grow rate of aphids	1	–
k	Carrying capacity of aphids	1	–
$f(y,z,r)$	Function of the cannibalism of larvae	–	–
c_i	Constant of the cannibalism function	–	1
ρ	Rate of acceptance of occupied patches by females	–	0·5

In order to simplify calculations, some parameters have been rescaled (third column), but for simplicity, we use the original notations in the rest of the paper. The last column shows the default values of the parameters that are used in simulations (unless specified otherwise).

$$\frac{dy}{dt} = m \cdot x - \gamma \cdot \mu \cdot r \cdot y - \xi \cdot y, \qquad \text{eqn 2}$$

where $\gamma \cdot \mu \cdot r \cdot y$ refers to the development of adults, which depends on the number of aphids the larvae eat, as shown by Dimetry (1976). The death rate of the larvae that hatch from the eggs is ξ. The dynamics of adult density is given by:

$$\frac{dz}{dt} = \gamma \cdot \mu \cdot r \cdot y - \varphi \cdot z, \qquad \text{eqn 3}$$

with φ the death rate of adults. Finally, we assume that in the absence of predators, aphid populations grow logistically. We assume that larvae and adults of ladybirds have different predation rates, denoted by μ and η respectively:

$$\frac{dr}{dt} = \alpha \cdot r \cdot \left(1 - \frac{r}{k}\right) - \mu \cdot r \cdot y - \eta \cdot r \cdot z. \qquad \text{eqn 4}$$

To improve the efficiency of the analysis, the model is rescaled in dimensionless parameters and densities. We rescale time from t to αt, i.e. relative to the growth rate of the aphids, and all densities to density/k, i.e. relative to the carrying capacity of the aphids. For ease of notation, we do not introduce new symbols for the scaled parameters, but refer to them by the original symbols, as introduced in eqns 1 to 4 (an overview is given in Table 1). This implies that the differential equations are the same as before, except for the population dynamics of aphids (eqn 4), which becomes:

$$\frac{dr}{dt} = r(1 - r) - \mu \cdot r \cdot y - \eta \cdot r \cdot z. \qquad \text{eqn 5}$$

This dynamical system can have three equilibria. The trivial equilibrium, where all densities are zero, is unstable for all positive parameter values. In the second equilibrium, the ladybirds are extinct and the aphid density is at its carrying capacity. In the third, the aphids and ladybirds coexist. It can be shown that in this case (see Appendix S1 for derivation):

$$\hat{r} = \frac{1 + \sqrt{1 + 4\left(\frac{\frac{\beta \cdot \eta}{\varphi} \frac{m}{(\lambda + m)}}{\frac{\gamma \cdot \mu}{\xi}}\right)}}{2\left(\frac{\beta \cdot \eta}{\varphi} \frac{m}{(\lambda + m)}\right)}. \qquad \text{eqn 6}$$

This equilibrium only exists if $\hat{r}$ is < 1, as otherwise the aphid density equals its carrying capacity, and there can be no coexistence. This leads to the condition:

$$2\left(\frac{\beta \cdot \eta}{\varphi} \frac{m}{(\lambda + m)}\right) > 1 + \sqrt{1 + 4\left(\frac{\frac{\beta \cdot \eta}{\varphi} \frac{m}{(\lambda + m)}}{\frac{\gamma \cdot \mu}{\xi}}\right)}, \qquad \text{eqn 7}$$

which can be written as:

$$\frac{\beta \cdot \eta}{\varphi} > \left(1 + \frac{\lambda}{m}\right) \cdot \left(1 + \frac{\xi}{\gamma \cdot \mu}\right). \qquad \text{eqn 8}$$

It can be concluded that β and η need to be high enough, and φ low enough, to make coexistence possible. In words, ladybird larvae have to eat many aphids and adults have to survive well and efficiently convert the aphids they eat into eggs. Figure 2a shows the maximum of the real part of the eigenvalues of the Jacobian matrices for the second (ladybirds extinct, aphids at carrying-capacity) and third equilibrium (coexistence) as a function of β, the rate of conversion of aphids into eggs by adult ladybirds. From this figure, it can be seen that as long as inequality (8) is invalid, the second equilibrium is stable. As soon as the third equilibrium exists, this non-coexistence equilibrium becomes unstable. Initially the third coexistence equilibrium is then stable, but at very high values of β it also becomes unstable. In that case none of the equilibria are stable. Numerical analyses show that in this region of the parameter space, there are stable limit cycles (Fig. 2b,c).

In biological terms, it simply means that ladybirds have to produce sufficient eggs to ensure coexistence. If egg production is larger, the model predicts limit cycles (Fig. 2b,d). Indeed increase in egg production leads to an increase in the number of larvae and of their predation rate, so the number
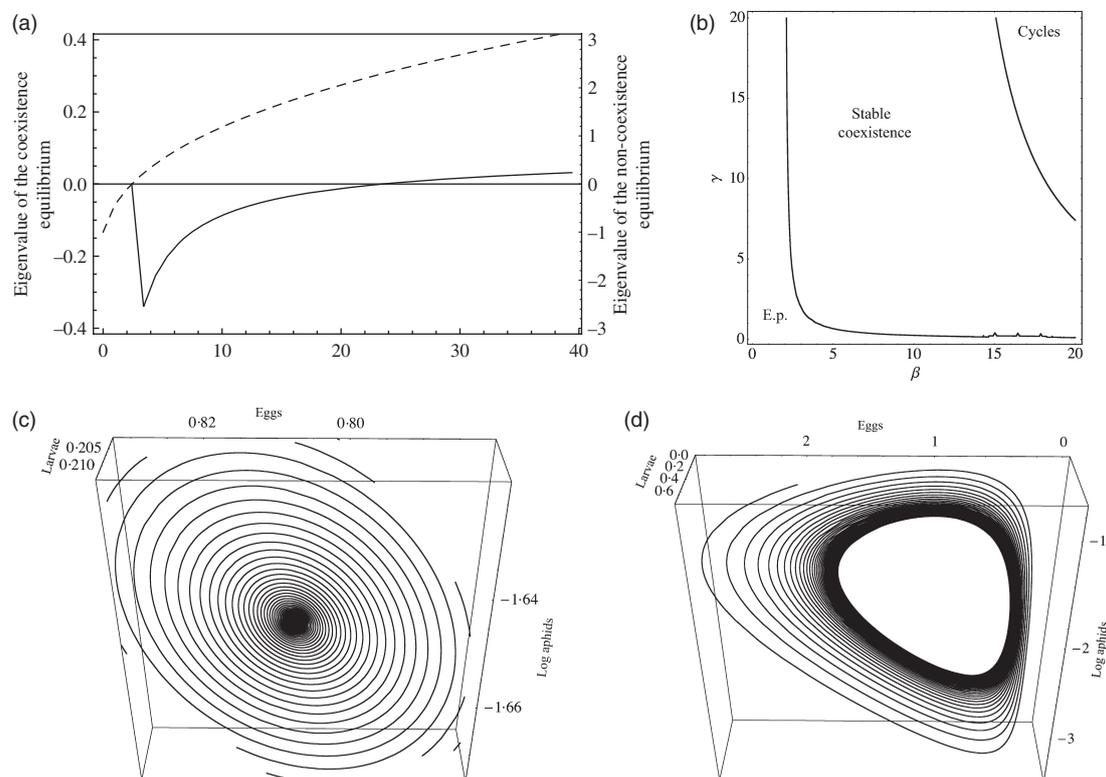
Fig. 2. (a) Maximum real parts of the eigenvalues of the non-coexisting equilibrium (dashed line) and the coexistence equilibrium (thick line). As long as inequality (8) is invalid, the co-existence equilibrium does not exist and the non-coexistence equilibrium is stable. This equilibrium becomes unstable as soon as inequality (8) holds, and at that point the coexistence equilibrium comes into existence and is initially stable. For large values of β, this equilibrium too becomes unstable and the system shows stable limit cycles. (b) Bifurcations of the system; e.p., extinction of predators. In this region aphid density is at its carrying capacity. At large values of β and γ stable limit cycles occur. (c) Example showing stability after damped cycles. Parameter values: $\gamma = 15$, $\beta = 14$. (d) Increase of fertility leads to stable cycles. Parameter values: $\gamma = 15$, $\beta = 17$.

of aphids per larva goes down. As we assume that the growth rate of larvae depends on the number of prey consumed, larvae will take longer to develop. This results in a decrease in adult recruitment.

Cannibalism model

Next, we consider a model where larvae also eat conspecific eggs (Fig. 1) In this case the egg density changes as follows:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \beta \cdot \eta \cdot r \cdot z - f(y,z,r) \cdot x \cdot y - \lambda \cdot x - m \cdot x, \qquad \text{eqn 9}$$

where $f(y,z,r)$ is the cannibalism function, defined by:

$$f(y,z,r) = c_1 \cdot \left(1 - \mathrm{e}^{-c_2 \cdot (y+z)}\right) \cdot \mathrm{e}^{-c_3 \cdot r}. \qquad \text{eqn 10}$$

c_1 is a constant that refers to the cannibalism tendency of the population. The term $\left(1 - \mathrm{e}^{-c_2 \cdot (y+z)}\right)$ models the effect of adult and larval densities on cannibalism. We assume that high adult and larval densities increase the risk of egg cannibalism, as the distribution of egg-batches becomes more aggregated due to the number of females that forage in the patch. Finally $\mathrm{e}^{-c_3 \cdot r}$ refers to the influence of aphid density on cannibalism. We assume that at high aphid densities there is less cannibalism, due to satiation of larvae and decreased probability of meeting eggs. For eggs, cannibalism can be

seen as an increase in the death rate, but it is a source of energy for the larvae. Accordingly, the dynamics of larval density is given by:

$$\frac{\mathrm{d}y}{\mathrm{d}t} = m \cdot x - \gamma \cdot (\mu \cdot r + f(y,z,r) \cdot x) \cdot y - \xi \cdot y. \qquad \text{eqn 11}$$

That is, the more conspecific eggs larvae eat, the more energy they accumulate and the greater their growth rate. As a consequence, the equation for changes in adult density becomes:

$$\frac{\mathrm{d}z}{\mathrm{d}t} = \gamma \cdot (\mu \cdot r + f(y,z,r) \cdot x) \cdot y - \varphi \cdot z. \qquad \text{eqn 12}$$

That is, the more conspecific eggs larvae eat, the higher the proportion that become adult. Egg cannibalism results in an increase in food supply and consequently decreases the time needed for larval development. Consequently, cannibalism first reduces the density of larvae (Fig. 3b), but this loss is not due to death but to an increase in adult recruitment (Fig. 3c). The resultant increase in egg production (Fig. 3a) is counterbalanced by cannibalism, which allows the system to reach equilibrium.

The conditions for the extinction of the predator do not change when cannibalism is added to the model. However cannibalism destabilizes the system, as it increases the para-
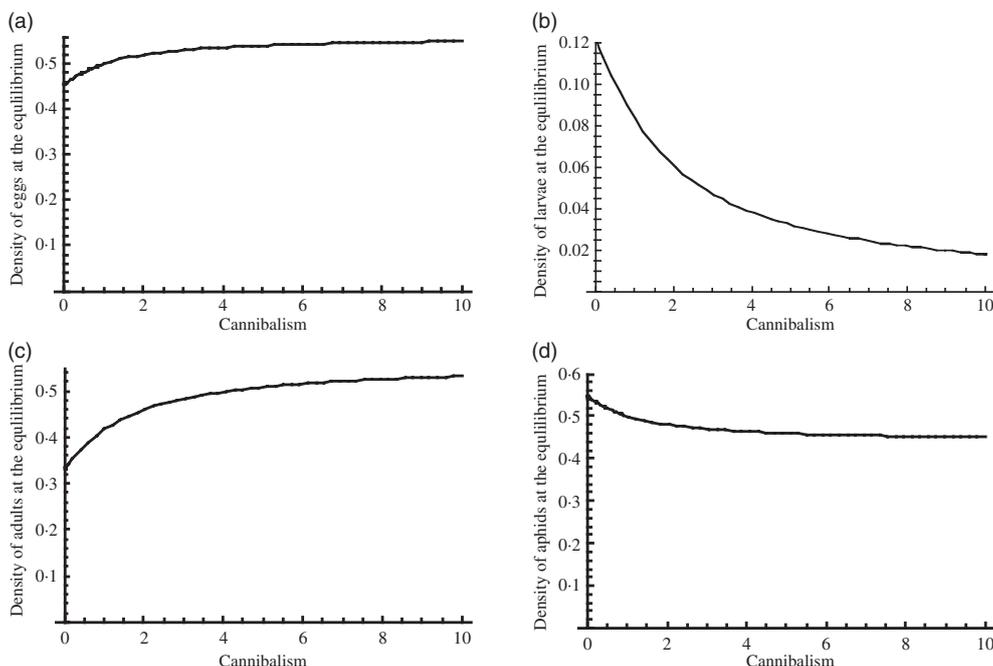
Fig. 3. Effect of cannibalism rate $f(y,z,r)$ on the steady states of the three stages of the predator (eggs, larvae and adults) and aphid density (a, b, c, d; respectively).

meter range over which cycling occurs (Fig. 4). Still the area of stable cycles remains limited, as a severe increase in the cannibalism rate does not lead to the disappearance of a stable coexistence area. In the following, only parameter combinations where stable coexistence occurs are considered.

Evolution of cannibalism. In this part we examine by means of adaptive dynamics how cannibalism might have evolved. We consider a resident ladybird population at equilibrium with a fixed level of cannibalism, and study whether a mutant with a
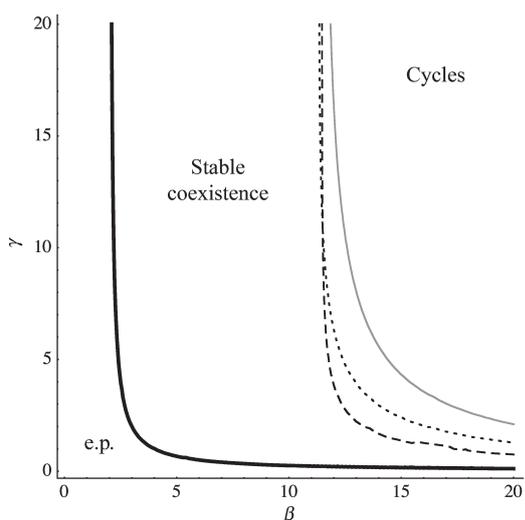
Fig. 4. Bifurcation diagram for the cannibalism model. As cannibalism increases, the area with stable limit cycles grows. But the range of parameter values that lead to the extinction of the predator remains the same; e.p., extinction of predators. Thick line: $f(y,z,r) = 0\cdot 2$; dotted line: $f(y,z,r) = 0\cdot 5$; dashed line: $f(y,z,r) = 2$.

slightly different tendency to cannibalize can invade the population. By determining which types of mutant can invade different types of resident populations, we can infer the direction of evolution (see e.g. Otto & Day 2007).

In this analysis we use the tendency to cannibalize as the decision variable that varies between mutant and resident. This implies that the parameter c_1 of the cannibalism function (cannibalism tendency, see eqn 10) will change for the mutant, and this will affect the invasive capacity of the mutant. We consider a resident population at equilibrium, with a cannibalism function, denoted by f_r. The dynamics of the egg density of a rare mutant appearing in this population is given by:

$$\frac{\mathrm{d}x_\mathrm{m}}{\mathrm{d}t} = \beta \cdot \eta \cdot \hat{r} \cdot z_\mathrm{m} - f_\mathrm{r}(\hat{y}, \hat{z}, \hat{r}) \cdot x_\mathrm{m} \cdot \hat{y} - \lambda \cdot x_\mathrm{m} - m \cdot x_\mathrm{m},$$

eqn 13

where $\hat{r}, \hat{y}, \hat{z}$ denote the equilibrium densities of aphids, larvae and adult ladybirds in the resident population respectively. Dynamics of mutant larva and adult densities are given by:

$$\frac{\mathrm{d}y_\mathrm{m}}{\mathrm{d}t} = m \cdot x_\mathrm{m} - \gamma \cdot (\mu \cdot \hat{r} + f_m(\hat{y}, \hat{z}, \hat{r}) \cdot \hat{x}) \cdot y_\mathrm{m} - \xi \cdot y_\mathrm{m}, \quad \text{eqn 14}$$

$$\frac{\mathrm{d}z_\mathrm{m}}{\mathrm{d}t} = \gamma \cdot (\mu \cdot \hat{r} + f_\mathrm{m}(\hat{y}, \hat{z}, \hat{r}) \cdot \hat{x}) \cdot y_\mathrm{m} - \varphi \cdot z_\mathrm{m}, \quad \text{eqn 15}$$

where $\hat{x}$ is the resident equilibrium egg density. Numerical analyses show that any resident population can be invaded by more cannibalistic mutants, that is, when $f_\mathrm{r}(\hat{y}, \hat{z}, \hat{r}) < f_\mathrm{m}(\hat{y}, \hat{z}, \hat{r})$. We have seen that despite the increase in cannibalism, the parameter range for coexistence of predators remains the same, as the loss of eggs due to cannibalism is counterbalanced by a better recruitment of adults (Fig. 3c). However, it can be seen from Figs 3b and 4 that without

limitation, the evolutionary increase in cannibalism would lead to a dramatic reduction in the density of ladybird larvae and the occurrence of cycles, with the stochasticity occurring under natural conditions, will increase the risk of extinction.

The ODP model

We now add the possibility of adult female predators responding to the presence of conspecific larvae and avoid laying eggs in such patches. The differential equations for the densities of the three predator stages become:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \beta \cdot \eta \cdot r \cdot z - \rho \cdot f(y,z,r) \cdot x \cdot y - \lambda \cdot x - m \cdot x, \qquad \text{eqn 16}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = m \cdot x - \gamma \cdot (\mu \cdot r + \rho \cdot f(y,z,r) \cdot x) \cdot y - \xi \cdot y, \qquad \text{eqn 17}$$

$$\frac{dz}{dt} = \gamma \cdot (\mu \cdot r + \rho \cdot f(y,z,r) \cdot x) \cdot y - \varphi \cdot z. \qquad \text{eqn 18}$$

With ρ the rate of acceptance of occupied patches, ($\rho < 1$), and should decrease when females become more sensitive to ODP. It can be seen that the incorporation of ODP in the relationship corresponds to a reduction in the cannibalism function. Therefore, the effect of ODP is opposite to cannibalism.

Evolutionary invasion analysis: adding ODP. We have seen that ODP can be considered as a decrease of the cannibalism function. To study its evolution, we proceed as before, and consider the initial growth rate of a rare mutant in a resident population fixed for a certain level of ODP. We suppose for physiological reasons that all larvae produce the molecules that compose the ODP, and that these molecules signal the presence of larvae. That is, a mature female will avoid laying eggs near larvae when they are able to detect them. The equations for the dynamics of rare mutants are as follows:

$$\frac{\mathrm{d}x_\mathrm{m}}{\mathrm{d}t} = \beta \cdot \eta \cdot \hat{r} \cdot z_\mathrm{m} - \rho_\mathrm{m} \cdot f(\hat{y},\hat{z},\hat{r}) \cdot x_\mathrm{m} \cdot \hat{y} - \lambda \cdot x_\mathrm{m} - m \cdot x_\mathrm{m}, \qquad \text{eqn 19}$$

where ρ_m is the rate at which mutant females lay eggs in occupied patches,

$$\frac{\mathrm{d}y_\mathrm{m}}{\mathrm{d}t} = m \cdot x_\mathrm{m} - \gamma \cdot (\mu \cdot \hat{r} + \rho_\mathrm{r} \cdot f(\hat{y},\hat{z},\hat{r}) \cdot \hat{x}) \cdot y_\mathrm{m} - \xi \cdot y_\mathrm{m}, \qquad \text{eqn 20}$$

where ρ_r is the rate at which resident females lay eggs in occupied patches, and

$$\frac{\mathrm{d}z_\mathrm{m}}{\mathrm{d}t} = \gamma \cdot (\mu \cdot \hat{r} + \rho_\mathrm{r} \cdot f(\hat{y},\hat{z},\hat{r}) \cdot \hat{x}) \cdot y_\mathrm{m} - \varphi \cdot z_\mathrm{m}. \qquad \text{eqn 21}$$

Numerical analyses show that mutants with a better recognition of ODP can invade a resident population. If the level of recognition can improve indefinitely during evolution, this will eventually lead to a perfect avoidance of occupied patches by females, reducing the level of cannibalism to zero.

Diversity model

From the previous analyses, we can conclude that there can be an arms race between the larvae and adult females. The best strategy for larvae is to mask their presence from gravid females and benefit by eating any eggs they lay. Thus, when adult females can detect the pheromone produced by larvae, there is a selective pressure towards changing the chemical composition of the pheromone. This situation gives the opportunity for polymorphism in ODP, since it is advantageous to produce a rare pheromone that cannot be detected by the majority of the females. On the other hand, the best response for adult females would be to recognize a mixture of molecules rather than only one, potentially at the cost of being less efficient at recognizing each molecule.

In order to explore this possibility, we consider a model with two versions of ODP and four phenotypes: AA, AB, BA and BB. The first letter refers to the version of ODP produced by larvae, the second to that recognized best by adult females. As before, ladybirds have three-age classes. When we add the dynamics of the aphid population, this results in a system of 13 differential equations. For example, the dynamics of the density of eggs of type AA are given by:

$$\frac{\mathrm{d}x_{AA}}{\mathrm{d}t} = \beta \cdot \eta \cdot r \cdot z_{AA} \\ - (\lambda + m + f(x_\mathrm{tot}, y_\mathrm{tot}, r) \cdot (\Gamma_{aa} \cdot (y_{AA} + y_{AB}) \\ + \Gamma_{ba} \cdot (y_{BB+BA}))) \cdot x_{AA}, \qquad \text{eqn 22}$$

where, e.g. Γ_{ba} denotes the rate of acceptance of patches with tracks of type B by females that are best at recognizing type A, and Γ_{aa}, Γ_{ab} and Γ_{bb} are defined analogously, with:

$$\Gamma_{aa} = \Gamma_{bb} \leq \Gamma_{ab} = \Gamma_{ba}. \qquad \text{eqn 23}$$

Now, we can write the equation for the dynamics of larval density of type AA as:

$$\frac{\mathrm{d}y_{AA}}{\mathrm{d}t} = m \cdot x_{AA} - \gamma \cdot (\mu \cdot r + f(x_\mathrm{tot}, y_\mathrm{tot}, r) \cdot (\Gamma_{aa} \cdot (x_{AA} + x_{BA}) \\ + \Gamma_{ab} \cdot (x_{BB} + x_{AB}))) \cdot y_{AA} - \xi \cdot y_{AA}, \qquad \text{eqn 24}$$

and for the adults as:

$$\frac{\mathrm{d}z_{AA}}{\mathrm{d}t} = \gamma \cdot (\mu \cdot r + f(x_\mathrm{tot}, y_\mathrm{tot}, r) \cdot (\Gamma_{aa}(x_{AA} + x_{BA}) \\ + \Gamma_{ab} \cdot (x_{BB} + x_{AB}))) \cdot y_{AA} - \varphi \cdot z_{AA}. \qquad \text{eqn 25}$$

Analysis of the model shows four kinds of stationary behaviour:

1. An equilibrium where the densities of all the phenotypes are the same.
2. An equilibrium where the densities of types AA and BB are equal and smaller than those of types AB and BA, which are also equal.
3. An equilibrium where the densities of AA and BB are equal and larger than those of AB and BA, which are also equal to each other.
4. Stable limit cycles, where the densities of all types fluctuate.

Equilibria (1) and (2) are unstable. Depending on initial conditions [and provided the starting conditions are not exactly equal to equilibrium (1) or (2)], the system converges to either case (3) or (4). Cycles are due to the alternation

of advantage due to cannibalism, and recognition of the ODP. That is, the sequences of the peaks are $AB \rightarrow AA \rightarrow BA \rightarrow BB \rightarrow AB$.

Alternation of peaks is the result of phases of high cannibalism alternating with phases of high recognition of ODP. When AB is dominant, it means that tracks are mainly of the kind A, but the recognition of ODP is not optimal. In this case, densities of type AA that is best at recognizing tracks of kind A increase, due to the avoidance of conspecifics. Phenotype BA is also better at recognizing A tracks, but it produces offspring that synthesize B tracks. Therefore, they are not recognized by their own group and are at a disadvantage compared to AA. When type AA is dominant, phenotype BA, whose larvae produce B tracks, are less likely to be recognized by the majority of the adult females and will benefit from eating eggs they lay. In the same way, BB and AB finally become successively dominant and close the cycle.

To obtain cycles, 'mixed strategies', i.e. AB (respectively BA) need to be frequent enough to increase at the time BB (respectively AA) dominates. Otherwise the system produces damped oscillations that go to the equilibrium (3) where both AA and BB are the main phenotypes. The higher the initial densities of AA or BB, the fewer are the oscillations. It means that in a scenario where ODP is well established, the model predicts the maintenance of a higher recognition rate for ODP when a mutant with new larval track is added in the system (Fig. 5).

Discussion

The models described in this paper were used to study the evolution of cannibalism in the context of the oviposition behaviour of aphidophagous insects. Although the models are clearly simplifications, this study leads to some interesting conclusions about the life-history evolution of aphidophagous predators.

Survival, when there is a lack of food that would result in extinction, is often cited as the reason for the evolution of cannibalism (Cushing 1991; Claessen, de Roos & Persson
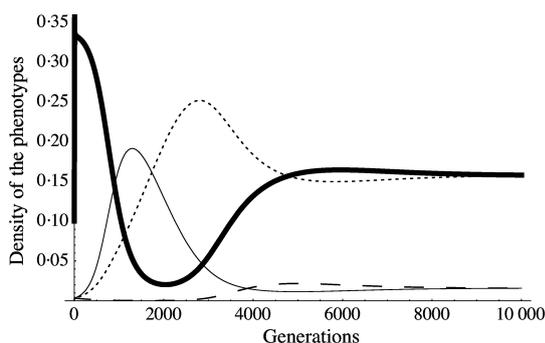
Fig. 5. Adult densities of AA, BB and AB. When we start with a high relative density of AA the system reaches an equilibrium where AA and BB are dominant. Starting values: $AA = 0{\cdot}1$, $AB = 0{\cdot}001$, $BA = 0{\cdot}001$, $BB = 0{\cdot}001$; $\Gamma_{AA} = \Gamma_{BB} = 0{\cdot}5$; $\Gamma_{AB} = \Gamma_{BA} = 0{\cdot}75$. Thick line: AA; thin line: BA; dotted line: BB; dashed line: AB.

2004). This study, however, indicates that in our case, a low density of aphids is not necessary for the evolution of cannibalism. The speed at which cannibalism evolved was probably greatly influenced by the ephemeral nature of aphid colonies as suggested by Wagner *et al*. (1999). Furthermore, our mutant invasion analysis shows that egg cannibalism should always be favoured by evolution. In nature, egg cannibalism mostly occurs when aphids are relatively scarce, at the beginning and at the end of an aphid colony's existence. Moreover, some laboratory studies have shown that cannibalism increases when aphid density is low. It is suggested that this simply results from the increased probability of larvae meeting conspecific eggs or larvae (Agarwala & Dixon 1992; Dixon 2000). So, we predict that, in the field, larvae will eat eggs whenever possible, whatever the availability of aphids. This prediction can explain for instance sibling cannibalism in which the first larva to hatch first eats its egg shell and then those eggs that have not yet hatched (Michaud & Grant 2004; Perry & Roitberg 2005). Gagne, Coderre & Mauffette (2002) show that neonate *Coleomegilla maculata lengi* Thimberlake prefer to eat eggs than aphids. Moreover, *A. bipunctata* fed a diet consisting exclusively of conspecific eggs have the same development time and weight gain as those fed only aphids (Agarwala & Dixon 1992; Michaud 2003). As larvae readily eat conspecific eggs, it is interesting to consider whether mothers could be selected to increase the food supply to first instar larvae by laying trophic eggs in unfavourable environments, as suggested by Perry & Roitberg (2005).

Although the loss of all the eggs to cannibalism is unlikely in the real world, too high a loss due to cannibalism could result in cycles. This result agrees with the prediction of some models that specifically study the influence of cannibalism on age-structured populations (see, e.g. Claessen *et al*. 2004 for a review). Under natural conditions, cycles might increase the risk of extinction. Consequently, in a persistent system, other factors not considered here might decrease the probability of larvae-encountering eggs. Possible factors are migration or selection at a metapopulation level, including extinction and recolonization. In addition, certain aspects of the behaviour of aphidophagous ladybirds may decrease the encounter rate. For instance, synchronous hatching of the eggs in clusters would restrict sibling cannibalism mostly to infertile eggs (Osawa & Ohashi 2008).

More generally, a female should detect the presence of larvae and so avoid ovipositing in colonies of aphids already being exploited. The sensitivity to these tracks should be under directional selection whatever the level of cannibalism. This explains why ODPs are recorded for many species of Coccinellidae and other aphid predators. Our model predicts that the evolution of ODP recognition should lead to the avoidance of occupied patches, implying the disappearance of cannibalism, due to a lack of opportunity. However, a mutant that would practice cannibalism and produce a different pheromone could invade a non-cannibalistic population.

As there is a conflict between larvae and adults in this respect, there is a selective pressure on the larvae to change the composition of their tracks in order to become less easily recognized by adults. This may lead to further diversification of the ODP. The *diversity* model with two types of ODP predicted that this could lead to a polymorphic equilibrium in which the mutant that is best at recognizing its own phenotype is the most frequent. This implies that adult females should be better at recognizing and avoiding the tracks of larvae of their own type. This result is counterintuitive as kin selection arguments lead us to expect that the best strategy for females is to avoid patches with larvae of the other type but not their own larvae. Indeed, as egg cannibalism is a source of food for the cannibals, it is more advantageous for females to have their eggs eaten by their own larvae than non-related ones. However, the probability of a female finding by chance a patch with its own larvae is probably weak because the residence time of a ladybird at a specific location in the field is on average not longer than 5–7 days in spring, and about 3 days in summer (Osawa 2000). Moreover during this time, ladybirds tend to frequently move within the habitat. In fact the emergence of larvae that produce a track that differs from that recognized by resident females would reduce the effect of the ODP, and as discussed above, a system with a low recognition rate of the ODP can be invaded by a mutant with a higher sensitivity. Therefore, we predict that females should be more sensitive to the tracks of closely related than to those of more distantly related larvae. The balance between the intensity of egg cannibalism, the sensitivity of females to ODP and changes in the chemical composition of this signal can account for the 50% egg cannibalism recorded in the field (Osawa 1993; Schellhorn & Andow 1999).

The following scenario is proposed for the evolution of ODP in Coccinellidae. On one hand, cannibalism has been favoured and has probably contributed to the success of sibfamilies as it has allowed higher reproductive rate at steady states. On the other hand, assuming cannibalism, females that could detect the presence of larvae and avoid occupied patches are likely to have had a selective advantage. Females could potentially respond to any chemical produced for any purpose by larvae and so avoid occupied patches. Such chemicals could for instance be produced by larvae to adhere to plant surfaces, or act as a waterproofing barrier (see Hadley 1981 for a review). As the avoidance of conspecific larvae results in a decrease in cannibalism, and egg cannibalism by the larvae should always be selected for (at least under the assumptions of our model), we can hypothesize that selection favoured quantitative or qualitative modifications of the mixture of molecules, as long as their function was maintained. As a result, the rate of recognition by females would have decreased and the probability of egg cannibalism would have increased. Finally, once different types of ODP had evolved, selection probably gave an advantage to those females able to recognize a mixture of hydrocarbons rather than a single molecule. We thus predict that females should be able to recognize mixtures of hydrocarbons, and that there should

be genetic variability in the type of chemical profile recognized, rather than in the ability to recognize a single compound. Our model also predicts that there should be frequent changes in the profile of larval tracks in populations and that females should be more sensitive to their own larval tracks than those of the larvae of other females.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Derivation to inequality (8).

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