

Prey Abundance, Intraguild Predators, Ants and the Optimal Egg-laying Strategy of a Furtive Predator

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Abstract Larval performance can have a great influence on female oviposition choice, especially in insects where the newly hatched offspring are unable to move any great distance to find an appropriate food source. For furtive predators, like the predatory midge *Aphidoletes aphidimyza* which preys on aphids while simultaneously residing and remaining undetected within their colonies, oviposition behaviour is crucial because these slow moving offspring are restrained to their natal colony. Here we develop a new model for predicting the optimum number of eggs that a furtive predator should lay in an aphid colony, based on: (1) the number of available prey (aphids); (2) the protection from predation conferred by “hiding” in the colony and (3) the effects of interspecific and intraspecific competition. We also explore the effect of aphid attendance by ants on oviposition behavior. We compare model predictions with empirical field observations of the clutch sizes of *A. aphidimyza* in apple orchards. The simplest of the four models best fits the observed data and provides the first field evidence that a furtive predator adjusts its clutch size as a function of prey density. The slope of the relationship between clutch size and aphid number is quite close to that predicted by our models suggesting that intra-clutch competition is the main factor governing furtive aphid midge oviposition choice.

Keywords Optimal egg-laying · intraguild predation · *Aphidoletes aphidimyza* · ants · furtive predation · Coccinellidae

Introduction

Oviposition behavior is central to investigations of insect population dynamics because it directly influences offspring survival and fitness. Important aspects of oviposition are the number of eggs laid in a patch, how egg and cluster sizes are

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determined and how patch quality is evaluated by the ovipositing female. This capacity to evaluate patch quality is crucial especially in insects whose newly hatched offspring are unable to move any great distance. Such offspring are limited to the patch chosen by their mother. Therefore, the link between female oviposition choice and larval performance is a crucial factor in the evolution of oviposition behavior (Thompson 1988; Craig et al. 1989).

Because aphid predators exploit patches in which aphid numbers fluctuate rapidly in time and space, they provide a good model to study insect oviposition strategy. Larval performance in aphidophagous predators varies with their predation behavior. Those with actively searching larvae (e.g. Coccinellidæ (Coleoptera), Chrysopidae (Neuroptera), Hemerobiidae (Neuroptera)) induce disturbances inside aphid colonies and are usually generalist predators with good dispersal capacities. Such active larvae can potentially find other aphid colonies or other prey when resources become depleted (Evans 2003). Consequently, eggs can be laid relatively far from aphid colonies. In contrast, furtive predators (e.g. Cecidomyiidae, Chamaemyiidae) produce small, relatively immobile larvae that live undetected within their prey colony (Lucas et al. 1998; Fréchet et al. 2008). Because they are small and have a reduced movement capacity, furtive larvae are highly dependent on their natal aphid colony for their survival and eggs must be laid near or inside an aphid colony (Lucas et al. 1998; Fréchet et al. 2008). Therefore, the oviposition decisions made by females are crucial because their fitness depends on their ability to determine which patches have the potential to sustain the development of their larvae.

Food patch quality generally decreases when other predatory individuals exploit it at the same time (Charnov's (1976) marginal value theorem). Many laboratory studies have demonstrated that active predators and parasitoids tend to minimize competition and avoid laying eggs in the presence of other predators or parasitoids (Hemptinne et al. 1992; Ruzicka 1997; Fréchet et al. 2006a,b; Wajnberg 2006). This should be particularly true for furtive predators because they are susceptible to intraguild predation by active predators (Lucas et al. 1998). However, furtive predators can gain protection from their own predators by "hiding" in their prey colony (Lucas and Brodeur 2001; Fréchet et al. 2008). This means that females may derive two advantages from laying eggs in colonies containing many aphids (more food and better protection from intraguild predators).

In the case of aphidophagous predators, a further complication arises because ants often protect aphid colonies from predators (Kaneko 2003; Katayama and Suzuki 2003; Stewart-Jones et al. 2007). If ants can't detect furtive predators in the colony they will indirectly protect them from other predators (Völkl 1992; Kaneko 2007). Guénard (2007) has shown that furtive predation can reduce the risk of being attacked by ants guarding aphid colonies. The effect of the presence of ants on furtive predator oviposition behavior has not yet been documented, but we predict that they should lay more eggs on colonies attended by ants because of indirect protection against active predators.

In the last 30 years, several models based on optimal foraging strategies have been developed to elucidate key factors involved in the oviposition decision-making process of parasitoids and active predators. The first models were based on the effects of external factors (number of aphids, aphid species, aphid size, colony age, presence of competitor or predators) on the decisions made by females (Parker and Courtney

1984; Godfray 1987; Charnov and Stephens 1988). Recent dynamic models have also demonstrated the importance of internal factors (eggs load, age, size and experience of the female) on the oviposition decision making process of parasitoids (Minkenberget al. 1992; Rosenheim 1999; Wajnberg 2006). Although oviposition behavior is crucial for furtive larva survival and fitness, few studies and no models deal with furtive predator oviposition behavior. We therefore produced a series of mathematical models predicting clutch size in a furtive predator exposed to a series of different constraints (aphids, conspecific and intraguild predator density, and presence of ants). We tested these predictions against observed clutch sizes of the furtive aphid midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) in nature.

The Models

We wish to predict the optimal number of eggs that a female aphid midge will lay in a given aphid colony as a function of the number of aphids, the number of intraguild predators in the colony and whether ants were present. Although dynamic models can include more factors and variability in oviposition behavior, we used simple static models by parsimony because predictions of oviposition behavior from dynamic models are very difficult to test in the field. They also need direct observation of the oviposition behavior of each female throughout her life.

Because furtive larvae live within aphid colonies through most of their larval stages, the amount of food, presence of intraguild predators, and intraspecific and interspecific competition within the colony should be the main factors determining the developmental success of a larval midge. To reflect these factors, our model is divided into three sub-equations: (1) effects of food availability, (2) competition, and (3) intraguild predation. Taking each component of the model separately, we first look at the effect of food availability. We suppose that the expected larval development success, F , of an egg laid in a given colony will depend, up to some limit, on the number of aphids in the colony. Larval developmental success is null if aphids are not sufficiently abundant to complete larval development, increases with aphid abundance and then reach a maximum (i.e. full success) regardless of how many aphids are present (Bouchard et al. 1988). This relationship can be modelled by a sigmoidal function of aphid abundance in the colony:

$$F = \frac{1}{1 + \exp(-R(A - a_h))} \quad (1)$$

where R is the rate, in days, of maturation (egg to pupa) which is constant in this case, A is the number of aphids in the colony and a_h is the number of aphids at which half of the maximum larval development success is achieved.

In the second component of the model, we expect that larval developmental success would be reduced by the effects of both intraspecific and interspecific (with intraguild predators) competition. We model this reduction as a proportion of the expected future reproductive success calculated in (1), the proportion being:

$$1 - \frac{Nz}{A} - \frac{Cy}{A} \quad (2)$$

where N is the number of aphid midge eggs in a given colony and z is the number of aphids that an aphid midge larva must consume to reach adulthood; C is the number of intraguild predators in the colony and y is the mean number of aphids that an intraguild predator consumes in an aphid colony. This expression assumes a linear competitive effect and resembles a Lotka-Volterra model in which the carrying capacity of the colony is determined by the number of aphids present and the competition coefficients depend on the minimum number of aphids eaten necessary to sustain a single individual. We did not use a nonlinear model because our data provide a good fit to the linear model. (Analysis of our data in a model with N raised to a power showed that the power did not differ significantly from 1 and the Akaike Information Criterion (AIC) values for the linear and nonlinear models differed by only 0.1 to 0.8%).

The final component of the model accounts for the effects of intraguild predation. We suppose that aphid midge larvae gain a dilution effect because they reside within an aphid colony (Lucas and Brodeur 2001). Assuming that intraguild predators have a type II functional response (which is often the case for such predators as ladybugs—see Agarwala et al. (2001) among others), we model the probability of being eaten by an intraguild predator as:

$$\frac{1}{\frac{1}{a} + T_h \times \frac{A}{C}} \tag{3}$$

where a is the attack rate of the predator and T_h is the handling time associated with each prey consumed. This assumes that midge larvae and aphids are consumed at the same rate.

Combining these three components we predict that, if a female aphid midge lays N eggs in a colony containing A aphids and C intraguild predators, she can expect to produce S adults in the next generation where S is given by:

$$S = N \frac{1}{1 + \exp(-R(A - a_h))} \left(1 - \frac{Nz + Cy}{A} \right) \left(\frac{1}{\frac{1}{a} + T_h \times \frac{A}{C}} \right). \tag{4}$$

By differentiating equation (4) by N , setting the derivative equal to zero and solving for N we can predict the optimal number of eggs which a female should lay in a given colony. This works out to:

$$\hat{N} = \frac{A}{2z} - \frac{z \times C}{2y} \tag{5}$$

We refer to this as the “*ant-free model*” of optimal clutch size. Interestingly, the first term of the equation (5) is the number of aphids in the colony divided by twice the number of aphids required to bring an aphid midge to maturity and the second term is the anticipated reduction in aphids eaten by intraguild predators also divided by two. This suggests that a female should estimate colony size and ensure there are twice as many aphids as necessary to bring all of the eggs she will lay to maturity and that she should discount her effort by twice the mean number of aphids that each intraguild predator will consume in an aphid colony.

To predict optimal clutch size when intraguild predators are absent, we remove the terms associated with intraguild predators and equation (4) reduces to:

$$S = N \frac{1}{1 + \exp(-R(A - a_h))} \left(1 - \frac{Nz}{A} \right) \tag{6}$$

and optimal clutch size in this “*predator-free model*” becomes:

$$\hat{N} = \frac{A}{2z}. \tag{7}$$

This prediction amounts to removing the competitive (second) term from equation (5).

To predict optimal clutch size when ants are present, we assume that the principal effect of ants for *A. aphidimyza* is to exclude intraguild predators. In this case, predictions for the “*ant-assisted model*” do not differ from the “*predator-free model*”:

$$\hat{N} = \frac{A}{2z}. \tag{8}$$

The above models assume that aphid midges do not adjust their clutch size to account for the presence of eggs laid in the colony by other conspecific females. However, *A. aphidimyza* secretes an oviposition-detering pheromone (ODP) that reduces the number of eggs laid by females that visit a colony in which aphid midge larvae are already present (Ruzicka and Havelka (1998)). To predict the optimal number of eggs a female should lay in a colony that already contains larvae, we modify the competition effect in expression (2) to become:

$$1 - \frac{(N + N_p) \times z}{A} \tag{9}$$

where N_p is a the number of *A. aphidimyza* larvae already present in the colony. Placing this in equation (6) instead of expression (2) we derive the predicted optimal clutch size as:

$$\hat{N} = \frac{A}{2z} - \frac{N_p}{2}. \tag{10}$$

We call this the “*subsequent clutch model*”. Here we again predict the female should ensure that there is twice the minimum number of aphids necessary to bring all her offspring to maturity, this time discounted by a share taken by conspecifics.

Finally, we model the hypothesis that females may anticipate competition with conspecific females and may thus adjust their clutch size to account for such future competition. Such a situation can be modelled using game theory (Maynard Smith 1976) based on the assumption that a female can anticipate that other females face the same constraints she does and will thus attempt to use a strategy which, if adopted by everyone, cannot be beaten by any other strategy (see Parker and Courtney 1984 for an example of predicting clutch size using game theory). In our case, we suppose that a female can estimate that some number of other females, N_f will lay eggs in the patch that she is about to exploit. We assume that these females will each lay an

average of n eggs in the colony. This will alter the force of competition in expression (2) to:

$$1 - \frac{z \times (N + n \times N_f)}{A} \quad (11)$$

To find the evolutionary stable strategy under these conditions (see Maynard Smith 1976, equation 2.11), we replace expression (2) by expression (11) in equation (6) and differentiate with respect to N . This gives the optimal clutch size of a female given the presence of N_f other females. Then, as we assume that all females are equal and face the same constraints we set $n = N$ and solve for N where the differential equals zero. This produces a predicted clutch size of:

$$N^* = \frac{A}{(2 + N_f) \times z}. \quad (12)$$

We call this the “*game theory model*”. Its prediction differs from the other models in that females should increase the proportion of extra food necessary to bring their offspring to maturity by a factor of two in the earlier models to a value that also depends on the number of females expected to lay a clutch in the colony. Earlier models accounted for competitive effects by subtraction.

Materials and Methods

To test our models we compared clutch sizes predicted by our models with the number of eggs laid in a given aphid colony on a given day. We conducted two field experiments at Mont Saint Bruno (Québec, Canada) (45°35' N, 73°21' W) from July 19 to 28, 2006 (first experiment) and from August 14 to 24, 2006 (second experiment). We used an apple orchard (348 m by 33 m) that had been abandoned since 1998 for the first experiment. The second experiment used an experimental orchard (57 m by 49.5) belonging to the «Institut de Recherche et de Développement en Agroenvironnement» in which pest control was practiced and from which apples were harvested. There was substantially more foliage on the trees in the second orchard compared to the first. There were also more green peach aphids (*Aphis pomi* De Geer (Homoptera: Aphididae)) in the second orchard.

In both experiments we first located aphid (*A. pomi*) colonies 1–2 m above the ground and mostly on the current year’s growth. We chose a number of colonies (69 for the first experiment and 101 for the second) as targets for our experiments. We deliberately chose colonies with a wide range in aphid number (from 5 to over 200) to test our prediction that aphid midges will adjust clutch size to the number of aphids present (by either equation (5), (7), (8), (10) or (12) representing the five predictions of our models). Prior to the experiment we removed all aphid midge eggs and larvae (16 *A. aphidimyza* (on 3 colonies) in the first orchard and 47 *A. aphidimyza* (on 22 colonies) in the second) from our target colonies. To test the first three models (“*ant-free model*”, “*predator-free model*” and “*ant-assisted model*”), we removed ants from many colonies so that two-thirds of the colonies were ant-free to test the “ant-free”

hypothesis. These colonies were maintained ant-free by applying “Tanglefoot ©” to branches leading to the colony daily and by daily visual inspection.

We started each experiment by introducing 250 aphid midge pupae (obtained from BIOBEST ©) at each of three points, 40 m apart, in the first orchard and two points, also 40 m apart, in the second. Using different release points allows the emerging adults to disperse and lay eggs in the entire orchard. We then observed the target colonies daily (except for two days in experiment 2 when thunder storms made field work impractical), counting (either by eye or using a 4 by 12 hand lens) the number of aphids, aphid midges (eggs and later larvae), intraguild predators and ants in each colony.

As the various models all take the form of linear regressions, data were analysed with regressions of the effects of aphid number, intraguild predator number and/or number of conspecifics already present on the number of aphid midge eggs in a clutch. Separate regressions were run with and without ants. We assumed that all eggs laid in a given colony on a given day came from just one female. This seems reasonable because only 6 to 8% of colonies received a new clutch per day making it unlikely that any one colony received eggs from more than one female. Moreover, the mean number of eggs per clutch (\pm SE) is 4.45 (\pm 2.8) for experiment 1 and 6.7 (\pm 6.2) for experiment 2 which fits with the mean number of eggs laid by a female per day (Havelka and Zemek 1999; Krivan and Havelka 2000; Jeoung et al. 2003).

Regressions were based on only the first clutch laid in each colony (and the number of aphids and intraguild predators present on that day) to preserve independence of observations. The exception to this was the test of the “*subsequent clutch model*” (equation 10) where we used the mean clutch size of subsequent clutches against mean aphid abundance and mean aphid midge larvae (already present) at the time of laying for each colony. The number of subsequent clutches laid (after the first) was used to calculate N_f in order to test the “*game theory model*” (equation 12). All measures of population size were square-root transformed to assure normality of errors and homoscedasticity. For all models, predictions depend on the value of z (number of aphids that an aphid midge larva must consume to reach adulthood) which is 12.5 *A. pomi* (Bouchard et al. 1988). Based on the square root transformation and the observation that aphid midge larvae must eat, on average 12.5 *A. pomi*, the predicted slope of the effect of aphid number on aphid midge clutch size in equations (5) and (7) is 0.2.

While linear regression was used to test for the existence of a relation between clutch size and aphid number, intraguild predator number and/or number of conspecifics already present, it was not appropriate for comparing observed slopes with those predicted by our four models. We tested our models by calculating slope and confidence intervals on the reduced major axis (Jolicoeur 1990) of our data, a more appropriate analysis when both variables in the relationship are measured with error. We accepted models for which the predicted slope was contained within the 95% confidence interval (indicated hereafter as CI95). We evaluated possible type II error by calculating the minimal confidence interval in which the predicted slope was contained.

To test whether the presence of ants affected clutch size, we used an analysis of covariance, with presence or absence of ants as a categorical variable and aphid

abundance as a measured variable. We used the statistical software package JMP IN 5.1 (SAS Institute 2001).

Results

We counted a total of 71 aphid midge clutches (316 eggs) in 69 colonies in experiment 1 and 159 (1075 eggs) in 101 colonies in experiment 2. We found intraguild predators in 115 colonies (41 for Experiment 1 and 74 for Experiment 2). In the first experiment only three colonies contained intraguild predators when the first clutch was laid in that colony so we were unable to evaluate the effect of these predators in this experiment. Coccinellidae (Coleoptera), mainly *Harmonia axyridis* Pallas, were the only intraguild predators observed. One ant species was present in our colonies, *Lasius niger* L. (Hymenoptera: Formicidae). When ants were present in a colony they stayed throughout a given experiment. The ratio ants/aphids was, on average, 1/10 for experiment 1 and 1/15 for experiment 2.

In experiment 2, in colonies with intraguild predators but no ants, aphid midge clutch size was positively correlated with aphid abundance ($p=0.02$, $R^2=0.47$, $N=13$) but not with intraguild predator abundance ($p=0.73$, $R^2=0.47$, $N=13$). In this case, we reject the “*ant-free model*”. In this analysis and in all that follow the intercept was not different from zero suggesting that clutch size was strictly proportional to aphid abundance.

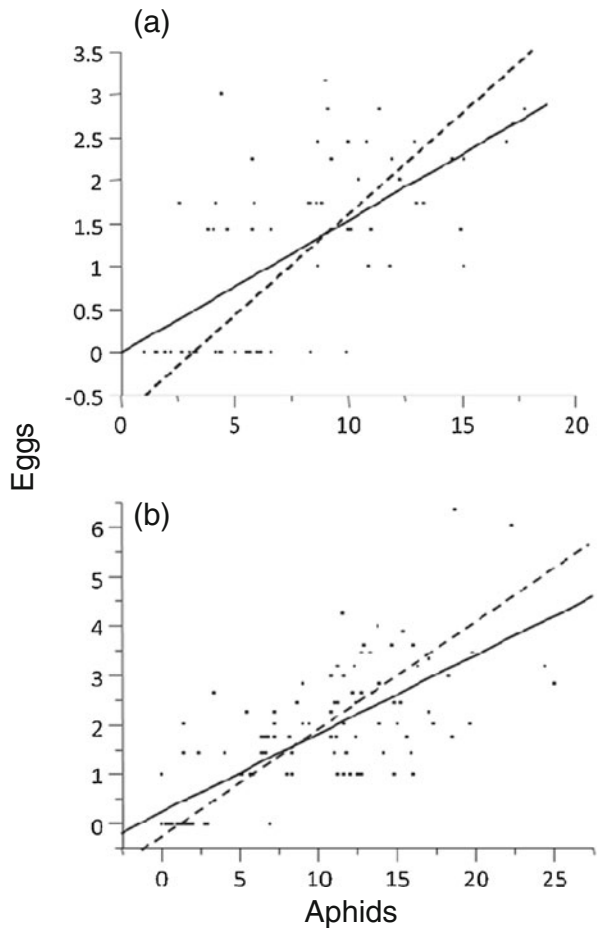
In both experiments, in colonies without intraguild predators and ants (“*predator-free model*”), aphid midge clutch size was positively correlated with aphid abundance ($p<0.0001$, $R^2=0.38$, $N=43$ for experiment 1 and $p<0.0001$, $R^2=0.59$, $N=55$ for experiment 2). We estimated the major axis slope as 0.22 (CI95 0.14 to 0.33) for experiment 1 and 0.20 (CI95 0.16 to 0.25) for experiment 2. Both were in close agreement with the prediction of 0.20 of the “*predator-free model*”.

In both experiments, in colonies attended by ants (“*ant-assisted model*”), aphid midge clutch size was positively correlated with aphid abundance ($p<0.0001$, $R^2=0.56$, $N=24$ for experiment 1 and $p<0.0001$, $R^2=0.48$, $N=33$ for experiment 2). We estimated the slope of the major axis as 0.26 (CI95 0.17 to 0.39) for experiment 1 and 0.22 (CI95 0.15 to 0.32) for experiment 2. This agrees closely with the predicted value of 0.20 from the “*ant-assisted model*”.

Ants had no effect on clutch size nor was there an interaction effect with aphid abundance (ANCOVA: Experiment 1, $p<0.0001$, $N=69$, $R^2=0.46$, ants: $p=0.11$, aphid abundance: $p<0.0001$, interaction ants \times aphid abundance: $p=0.23$; Experiment 2, $p<0.0001$, $R^2=0.54$, $N=101$, ants: $p=0.94$, aphid abundance: $p<0.0001$, interaction ants \times aphid abundance: $p=0.80$). Estimates for the major slope axes calculated using the entire data set are 0.23 (CI95 0.18 to 0.32) in experiment 1 and 0.22 (CI95 0.18 to 0.26) in experiment 2. These were close to the predicted value of 0.2 predicted by the “*predator-free model*” and the “*ant-assisted model*” (Fig. 1).

To test the “*subsequent clutch model*” we regressed the mean clutch size of subsequent clutches against mean aphid abundance and mean aphid midge larvae (already present) at the time of laying. In this and subsequent analyses we did not include intraguild predator abundance or the presence of ants because these factors

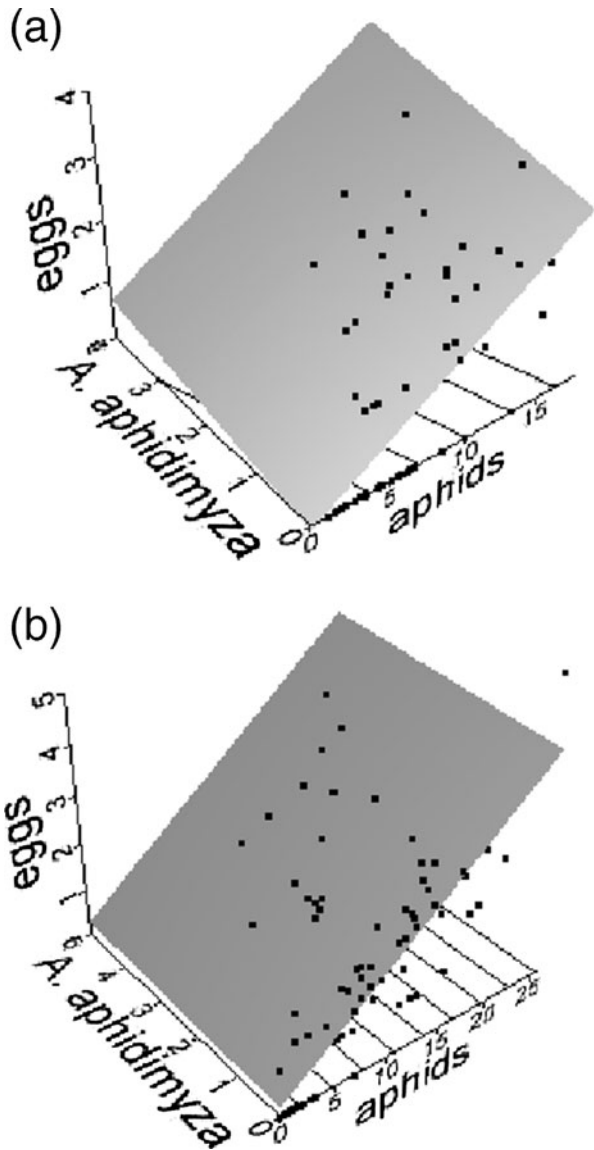
Fig. 1 Linear (solid line) and reduced major axis (dotted line) regressions of midge clutch size as a function of the number of aphids per colony using all colonies from experiment 1 (a) and from experiment 2 (b). Data on both axes are square root transformed to ensure normality of residuals. For the linear regression $R^2=0.43$, $N=69$ and $p<0.0001$ for experiment 1 (a) and $R^2=0.54$, $N=101$ and $p<0.0001$ for experiment 2 (b). Neither y intercept differs significantly from zero ($p=0.99$ in experiment 1 and $p=0.15$ in experiment 2)



had no influence in the earlier analyses. When aphid midge larvae were already present in a colony, clutch size was still positively correlated with aphid number but was not affected by the number of conspecifics already present (Experiment 1, $R^2=0.52$, $N=69$, $p<0.001$ for aphid abundance and $p=0.15$ for conspecifics abundance; Experiment 2, $R^2=0.66$, $N=101$, $p<0.001$ for aphid abundance and $p=0.79$ for conspecifics abundance) (Fig. 2). Moreover, we tested the effects of removing indigenous aphid midges from colonies prior to the start of the experiment and we found no effect of indigenous midges on clutch size as a covariate of aphid abundance. For experiment 1, we found indigenous aphid midges in only three colonies which did not allow us any statistical analysis. For experiment 2 ($R^2=0.55$, $N=101$, d.f.=98 for the overall model) the effect of aphid number was significant ($p<0.001$) while the effect of indigenous aphid midge was not ($p=0.13$). We thus reject the “subsequent clutch model”.

The “game theory model” predicts a different slope from those derived in the other models. In experiment 1, we observed 27 subsequent clutches and 44 colonies that

Fig. 2 Regression of midge clutch size as a function of the number of aphids per colony and the number of conspecific larvae already in the colony for experiment 1 (a) and experiment 2 (b). Data are square root transformed to ensure normality of residuals. For experiment 1, $R^2=0.52$, $N=69$ and $p<0.001$ for the effect of aphids, $p=0.15$ for the effect of conspecifics (*A. aphidimyza* larvae). For experiment 2, $R^2=0.66$, $N=101$ and $p<0.0001$ for the effect of aphids and $p=0.79$ for the effect of conspecifics (*A. aphidimyza* larvae)



received an initial clutch producing a value of $N_p=0.61$ and a predicted slope of 0.175. In experiment 2 we observed 80 subsequent clutches in 78 colonies which received an initial clutch producing a value of $N_p=1.01$ for a predicted slope of 0.162. We compared these predicted slopes with those estimated in the major slope axes two paragraphs earlier (estimated slope value: 0.23 (CI95 0.18 to 0.32) in experiment 1 and 0.22 (CI95 0.18 to 0.26) in experiment 2) and found that they do not fall within the 95% confidence interval for the observed data. The “game theory model” is thus also rejected.

Discussion

Optimality models predict that females should adjust their egg laying behavior in response to patch quality. For aphidophagous predators, patch quality depends mainly on the presence of competitors and the number of aphids because aphids are gregarious. Using the marginal value theorem one can predict that active predators and parasitoids should lay more eggs or spend more time in high-density aphid colonies (Evans 2003; Wajnberg 2006). The close correspondence between the predicted slopes of our models (“*predator free model*” and “*ant-assisted model*”) and slopes estimated from our field results provides the first field evidence of a furtive predator adjusting its clutch size in response to aphid density. Moreover, this response follows the predicted slope, which provides for twice the minimum amount of food necessary to bring offspring to maturity, as predicted by our optimization model (parameter z in our models). That these two models best fit our data suggests that, for furtive predators, intraclutch competition is the main factor governing optimal clutch size. While, we cannot exclude other factors which might explain the tight fit between our field observations and our data, we believe that intraclutch competition is the most parsimonious and probable explanation. For active predators, studies have also demonstrated that female oviposition behavior is governed by the necessity of minimizing the risk of competition between larvae (Oliver et al. 2006; Seagraves 2009). This is because aphid populations persist only for short periods (Dixon 1959) and the development time of active predators (approximately one month) is much longer than those of their prey (Dixon et al. 2005). Although the larval development of furtive predators is shorter (Havelka and Zemek 1999), the same selective pressure should drive their oviposition behavior. Moreover, intraclutch competition should be important for furtive predators because, in contrast to active predators, furtive larvae must develop in the aphid colony chosen by the female because larvae are not sufficiently mobile to change of colony.

Although *A. aphidimyza* seems to adjust clutch size to minimize intraclutch competition, they do not adjust for the presence of offspring of conspecific females. Many laboratory studies show that active predators such as female ladybirds and lacewings avoid laying their eggs in aphid colonies in the presence of conspecifics or conspecific cues to minimize competition and cannibalism (Hemptinne et al. 1992; Ruzicka 1996; Fréchet et al. 2003). However, our study of *A. aphidimyza*, in nature, did not show this reaction (Fig. 2, “*subsequent clutch model*”, “*game-theory model*”). This occurs despite Ruzicka and Havelka’s (1998) observation that, in the laboratory, larvae of *A. aphidimyza* secrete an “Oviposition Detering Pheromone” (ODP) that effectively deters conspecific females from ovipositing on aphid-infested plants. However, in the laboratory experiment, *A. aphidimyza* females were confined in experimental arenas and test plants were contaminated by 30 or 50 third-instars *A. aphidimyza* larvae, which is six to ten times greater than the larval density in our experiments. Moreover, in nature, the effectiveness of pheromones is reduced by wind, rain, and ultra-violet light (Marchand and McNeil 2000). This suggests that female response to ODP can differ between laboratory and natural conditions. Further behavioural experiments are needed to investigate more precisely the reasons and mechanisms underlying this difference.

Previous studies have postulated that females should lay fewer eggs in colonies also exploited by intraguild predators (Ruzicka 1997; Agarwala et al. 2003). As the

aphid midge oviposition strategy seems to be finely attuned to aphid abundance, it was surprising to find no evidence that they respond to the presence of intraguild predators. Lucas and Brodeur (1999) also found that aphid midges do not adjust oviposition to the presence or absence of intraguild predators. On the other hand, Ruzicka and Havelka (1998) found, in a laboratory study, that aphid midges laid fewer eggs on plant contaminated by intraguild predator larval tracks. However, this response depended on intraguild predator species and, Ruzicka and Havelka (1998) used a high number (i.e. 20 to 30) of intraguild predator larvae to contaminate plants before oviposition tests. In our experiments, it is possible that, (1) our small sample size (aphid midges laid eggs only 13 times in colonies containing intraguild predators) prevented us from detecting a reaction to predators; (2) *A. aphidimyza* do not respond to *H. axyridis* (i.e. the main intraguild predator observed in our experiments) presence or larval tracks (response not tested by (Ruzicka and Havelka 1998)).

It is interesting that *A. aphidimyza* females laid twice the number of aphids needed for larval development. This suggests that food may not be the only consideration in determining the number of eggs to lay. *A. aphidimyza* larvae may use the excess prey for their dilution effect, thus reducing exposure to intraguild predation (Lucas et al. 1998). Further studies might evaluate the possibility that midges assess not only the number of intraguild predators present but also the number likely to arrive before her larvae mature.

Furtive midges did not adjust their clutch sizes in the presence of ants. The main effect of ants on aphid colonies is to remove active predators thus protecting the aphids (Kaneko 2003; Stewart-Jones et al. 2007) and, potentially, their furtive predators (Guénard 2007). This absence of reaction to the presence of ants may be the result of a general absence of reaction to predators or may reflect a cost for furtive larvae to exploit an aphid colony attended by ants. There may even be a risk that ants will prey on aphid midges (adults and/or larvae) as they do sometimes on aphids (Guénard 2007). However, aphid midges usually lay eggs at dawn and dusk while ants are most active during the day, so the latter are unlikely to interfere with the egg-laying process.

Our results demonstrate that midges lay optimally in aphid colonies regardless of conspecifics, intraguild predators and ants. The close correspondence between our field results and our model ("*predator free model*") predictions suggests that aphid midges are skilled at evaluating aphid colony size and adjust their clutch size to optimize survival and reproductive success of their offspring. Moreover, our field results demonstrate that the amount of food necessary to bring offspring to maturity determines the number of eggs laid in a colony. This is consistent with optimal foraging theory and findings of previous studies (Lack 1947; Charnov 1976; Parker and Courtney 1984).

We chose not to use dynamic modelling to predict furtive predator oviposition behavior although such models have been used for parasitoid behavior. In contrast to our models, dynamic models could include internal effects of such as egg load, age and experience of the female (Wajnberg 2006). Many studies have shown that these factors could have an important influence on parasitoid oviposition strategy (Minkenberget al. 1992; Wajnberg 2006) but there are no similar studies for furtive predators. Furthermore, in contrast with our study, very few studies have tested dynamics models in nature because of the complexity of the assumptions and predictions

involved. In addition, our model is effective for predicting furtive predator clutch size in nature suggesting that the additional complexity of dynamic modeling may not be necessary. Other studies have demonstrated that although static models ignore a great deal of variability in behavior they still produce a cost estimate that is approximately correct as a mean expectation of lost future reproduction (Mangel 1989; Rosenheim 1999).

In summary, our study provides, to our knowledge, the first models of furtive predator oviposition behavior. By comparing our models' predictions to field results we show, for the first time in nature, that a furtive predator adjusts its clutch size to aphid density, probably minimizing intraclutch competition. This contrasts with the oviposition behavior of active predators in that the latter adjust oviposition to the presence of conspecifics while our furtive predator did not.

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