

**A model to describe the reproductive rate in the aphid *Sitobion avenae*
(Hemiptera: Aphididae): A case study**

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Abstract. The development of a detailed population dynamics model to simulate changes in grain aphid (*Sitobion avenae* F.) populations on wheat in field conditions requires the identification of every component of the system. The present study proposes a deterministic model for the fecundity function. An optimality theory is applied here to model aphid reproduction in order to obtain a usable mathematical description of larvae laying rate. This rate is assumed to be mainly dependent on temperature since this effect is commonly observed in poikilothermic organisms. It is taken into account by using a thermodependent physiological time scale for measuring adult age. The resulting function is fitted with two data sets. Despite some bias, which is discussed, the model matches relatively well with the observations. The model framework may be easily extended to other species.

INTRODUCTION

The general purpose of this study is to develop a detailed mechanistic model – with continuous time and age variables – to simulate the population dynamics of the grain aphid (*Sitobion avenae* F.). Such a model is required for understanding the evolutionary biology of aphids, i.e., the model parameters should be related directly to life history traits of aphids, in order to put forward and test some hypotheses about the action of natural selection. The focus of the study is fecundity function because (a) it is one of the most important components of such a model and (b) other factors, such as ageing or moult functions, are comparatively better known (Dean, 1974; Kieckhefer et al., 1989; Pierre, 1990). In most examples, the vital rates of poikilothermic organisms are known to be mainly dependent on temperature. Therefore, the reproductive function is attributed to be temperature-sensitive by introducing a thermodependent ageing rate for adults. Following Curry & Feldman (1989), it is assumed that temperature has a two-fold influence on the fecundity rate through its modification of the metabolic rate of adults and its determination of the total amount of an individual's potential progeny.

The model presented here is based on a hypothesis of optimality of life history traits, which assumes that organisms increase their fitness by optimising resource allocation to growth, survival and reproduction from birth to death. Such a mechanism determines both the age and size at maturity and the number of offspring produced at each age under the assumption of trade-offs between current reproduction and expected subsequent reproduction of adults (Stearns, 1992). The shape of the function describing the age-dependent

larvae laying rate will be a consequence of the allocation of resources between the various components. For such studies, aphids are organisms of great interest because they have developed many original adaptive traits such as viviparity, parthenogenesis, alternation of sexual and asexual phases and intra-clonal polyphenism (Moran, 1992). Moreover, aphids are of economic interest as one of the most important group of agricultural pests in temperate areas. Due to their pest status, the biology of aphids is fairly well known and many data are available. However, very few studies examined the fecundity function of aphid. Functions proposed by Bieri et al. (1983) and Simon et al. (1991) are not suitable for our purpose, since they are not expressed on a physiological scale and may not be generalised easily and extrapolated to various experimental conditions. In addition, such models are highly empirical and may not be related clearly to biological aspects. Kindlmann, Dixon and co-authors have studied the reproduction of aphids from an evolutionary viewpoint and the present investigation is based on their work (Kindlmann & Dixon, 1989; Dixon et al., 1993). However, their studies did not optimise daily fecundity (Kindlmann et al., 1992). This study evaluates the extent to which the observed timing of larvae laying is consistent with the results predicted by the life history theory, and whether theoretical assumptions are helpful for quantitative prediction of aphid reproductive rates. At any age, the fraction of resources devoted to reproduction may be invested preferentially either in the growth of the more mature embryos (current reproduction) or in the growth of those younger as well as in new ovulations (future reproduction). Based on these theoretical considerations, a mathematical model was designed and then fitted to experimental data in order to test the validity of our hypotheses.

THEORETICAL BASIS OF THE MODEL

Observed dynamics of larvae laying

The general features of the mean daily fecundity variation of apterous aphids and winged aphids are relatively constant in all species studied (Bieri et al., 1983; Curry & Feldman, 1987; Simon et al., 1991). For apterous aphids, the curve showed a short initial period of increase, followed by a relatively rapid decrease, depending on temperature and environmental conditions. In alates, the curve was similar, except that the initial phase of increase was generally missing. Under favourable conditions, temperature was the most important factor acting on the determination of daily fecundity. Temperature appeared to have no influence on the general shape of the curve but, under high temperature, reproductive life was shortened and the mean daily production was augmented. This suggests that the larvae laying rate may be modelled by a single function at any given temperature, if expressed on an appropriate physiological age scale. In this study, apterous morphs of aphids are used.

Basic assumptions

Kindlmann & Dixon (1989) showed the existence of a constraint on the maximal gonadal growth rate of aphids. According to them, if the soma size becomes too large, in relation to the gonadal size, then a proportion of the assimilated energy may not be invested in gonadal growth. Therefore, aphids reproduce singly, rather than in clutches. If there is a physiological constraint on the growth rate of the more mature embryos, the growth rate of young embryos would be limited by the necessity of preserving a minimal time lag between successive larvipositions. Thus, both the age distribution and the total number of embryos should be optimal (related to the optimal gonad size), the former remaining virtually stable throughout the reproductive life. This is in agreement with the observations for *Sitobion avenae* (Caillaud et al., 1994). Moreover, it might explain the maintenance of ovulation activity as a means of preserving the optimal age distribution of embryos. Such activity would cease when the increase of mortality rate, as well as the reduction of the metabolic efficiency of adults, result in a marked decrease in the probability of new

embryos completing their development. The phenomenon might even be inverted and become negative in the case of resorption of embryos (Ward & Dixon, 1982).

Form of the fecundity function

The stability of embryo age distribution implies that the number of embryos that reach maturity at any time is proportional to the current gonadal size. If $\beta(t)$ is the content of the ovarioles at time t , $n(t)$ is the cumulative total number of larvae born from the onset of the reproductive period to time t and $f(t)$ is the individual mean larvae laying rate at time t , then

$$\frac{dn}{dt} = f(t) = k \cdot \beta(t) \quad (1).$$

If we assume there is neither embryo resorption nor new ovulation from the onset of reproduction, then

$$\frac{d\beta}{dt} = -\frac{dn}{dt} = -f(t) \quad (2).$$

From (1) and (2)

$$\frac{df}{dt} = -k \cdot f(t) \quad (3),$$

the solution of which is

$$f(t) = \Phi_0 \cdot e^{-k(t-t_0)} \quad (4)$$

where Φ_0 is the initial larvae laying rate (larvae laying rate at time $t = t_0$).

According to equation (4), $f(t)$ is a monotonously decreasing exponential function. This contradicts the usual shape of observed data and some of our observations that suggest the existence of new ovulation after the onset of reproduction (Leather, 1983; Caillaud et al., 1994). It may be explained by the need to keep an optimal distribution of the embryo age structure. Then (2) becomes

$$\frac{d\beta}{dt} = -f(t) + r(t) \quad (5)$$

where $r(t)$ is the individual ovulation rate at time t , and (3) becomes

$$\frac{df}{dt} = k \cdot [-f(t) + r(t)] \quad (6).$$

Solutions of this equation are

$$f(t) = g(t) \cdot e^{-k \cdot t} \quad (7)$$

with

$$g(t) = k \cdot \int r(t) \cdot e^{k \cdot t} dt \quad (8).$$

Very little is known about the function $r(\cdot)$, but some general assumptions can be made: (i) $r(\cdot)$ decreases later in the adult's life and (ii) $r(\cdot)$ is positive, at least during the first period (since negative ovulation activity implies embryo resorption).

For practical reasons of parameter estimation and to achieve a good agreement with the observed data, we chose the function

$$r(t) = \frac{a}{t+b} \cdot e^{k \cdot t} \quad (a, b > 0) \quad (9).$$

Accordingly, equation (7) becomes

$$f(t) = k \cdot a \cdot \ln(t+b) \cdot e^{-k(t-t_0)} \quad (10).$$

Modelling the influence of temperature

In principle, temperature (θ) has two effects on fecundity. It interferes with the determination of instantaneous fecundity, $f_\theta(t)$, by acting on adult ageing rate, $R[\theta]$, as well as by having some influence on the mean total amount of offspring, $FT(\theta)$. The first effect can be taken into account by measuring time on an appropriate physiological age scale. If the physiological age of an aphid, at time t , is $x(t)$, then

$$x(t) = \int_{t_0}^t R[\theta(u)] du \quad (11)$$

where $\theta(u)$ is temperature at time u , $R[\theta]$ is the ageing rate at temperature θ , and t_0 is the time of the adult moult.

Since $FPT(\theta)$, the total potential fecundity (independent of the expectation of life) under temperature θ , was defined as

$$FPT(\theta) = \int_{t_0}^{\infty} f_\theta(u) du \quad (12),$$

then

$$p_\theta(x(t)) = \frac{f_\theta(x(t))}{FPT(\theta)} \quad (13)$$

where $p_\theta(x)$ is the instantaneous fraction of reproduction achieved at age x , at temperature θ . To simplify the notation, the fecundity function indicated by $f(\cdot)$ is either a function of physiological age, x , or of time, t , according to the context. Following Curry & Feldman (1989), we assume that

$$\forall \theta_1 \text{ and } \theta_2, p_{\theta_1}(x) = p_{\theta_2}(x) = p(x).$$

This means that the fraction of total potential reproduction achieved at age x is independent of temperature. Hence,

$$f_\theta(x) = \text{FPT}(\theta) \cdot p(x) \quad (14)$$

and, from (10),

$$f_\theta(x) = A \cdot K \cdot \text{FPT}(\theta) \cdot \ln(x+B) \cdot e^{-Kx} \quad (15).$$

According to this model, the effect of temperature on metabolic rate is accounted for entirely if data is expressed on an appropriate physiological time scale.

Determination of physiological age

In the present model, time is measured on a physiological age scale [equation (11)]. The aphid ageing rate, $R[\cdot]$ is assumed to be temperature-dependent, $R[\theta(t)]$. We define $R[\theta] = \frac{1}{D_{50\%}(\theta)}$, where $D_{50\%}(\theta)$ is time needed to achieve 50% of reproduction potential under temperature θ . The calculation of $D_{50\%}(\theta)$ is given below.

Estimation of the total potential fecundity $\text{FPT}(\theta)$

The value of $\text{FPT}(\theta)$ is close to $\text{FT}(\theta)$ under favourable conditions. According to the literature, $\text{FT}(\theta)$ appears to be dependent on various factors other than temperature, such as host plant species and its phenological stage (Watt, 1979; Di Pietro & Akli, 1987; Kieckhefer & Gellner, 1988), wheat cultivar (Di Pietro & Akli, 1987; Caillaud et al., 1994), aphid clone (Simon et al., 1991; Markkula & Pulliainen, 1965), aphid morph (Simon et al., 1991; Wratten 1977), adult body size (Wratten, 1977), differences in ovarioles number (Leather & Wellings, 1981), or generation from which individuals arise (i.e., during spring, summer or autumn, Wellings et al., 1980). In many examples, experimental conditions appeared to be as important in the determination of $\text{FT}(\theta)$ as the factors mentioned above. Consequently, since the mechanism controlling the FT value is known poorly, it was considered inappropriate to model FT on the basis of our results. In addition, the possible direct influence of temperature on this parameter has yet to be established. If any, its effect should be negligible in comparison with the direct acceleration of metabolic rate. Therefore, it was thought preferable to denote total fecundity and total potential fecundity by $\text{FT}(\Psi)$ and $\text{FPT}(\Psi)$, respectively, where Ψ is the state of environmental conditions at a given date. $\text{FPT}(\Psi)$ may be considered as a constant (mathematical expected value) or as a random variable with a distribution yet to be determined or as a deterministic function. This is so provided the relevant environmental characteristics may be related to the total potential fecundity.

MATERIAL AND METHODS

Calculation of $\text{FPT}(\Psi)$, $D_{50\%}(\theta)$ and the $p(\cdot)$ and $f(\cdot)$ functions

The value of $\text{FPT}(\Psi)$ in this study corresponds with the total amount of offspring expected to be produced by an individual whose death happens after the end of the reproductive period:

$$\text{FPT}(\Psi) = \sum_k \left(\frac{1}{N(t_k)} \cdot \sum_{i=1}^{N(t_k)} f_i(t_k) \right) \quad (16)$$

where $t_1, \dots, t_k$ are observation dates, $f_i(t_k)$ is the amount of offspring produced by the i^{th} individual between t_{k-1} and t_k , per unit time, and $N(t_k)$ is the number of living aphids at time t_k .

Let $z_k = \frac{t_k - t_{k-1}}{2}$ and $\Delta x_k = x(t_k) - x(t_{k-1})$. The fraction of fecundity achieved during a short period Δx is near $p(x) \cdot \Delta x$. Hence, $p(\cdot)$ can be estimated for x values corresponding to z_k by

$$p(x(z_k)) = \frac{1}{N(t_k) \Delta x_k} \cdot \sum_{i=1}^{N(t_k)} \frac{f_i(t_k)}{\text{FPT}(\Psi)} \quad (17).$$

Then, according to (14),

$$f(x(z_k)) = \text{FPT}(\Psi) \cdot p(x(z_k)) \quad (18).$$

Finally, $D_{50\%}(\theta)$ was set to the smallest value, t_s , for which $p(x(t_s)) \geq 0.5$.

This choice of procedure prevented the underestimation of key parameters in the model due to the fact that some individuals die before achieving their total potential fecundity (censored data). The observed values of $\text{FPT}(\Psi)$, $\overline{\text{FT}}(\Psi)$ (mean total amount of offspring), $D_{50\%}(\theta)$, and $\overline{D}_{50\%}(\theta)$ (mean time needed to achieve 50% of total amount of reproduction) are summarised in Table 1. $\overline{\text{FT}}(\Psi)$ and $\overline{D}_{50\%}(\theta)$ are also reported in order to allow some comparisons to be made with data from other authors.

From a practical point of view, it is of interest to obtain an estimation of the function $R[\theta]$, i.e. of the relation between this parameter and temperature. Throughout the observed temperature range (10°C–25°C), this relation is roughly linear. Thus, it was modelled using the classical linear day-degree model: $R(\theta) = \frac{1}{K_T} \cdot \sup[\theta - \theta_0, 0]$. In our study, $\theta_0 = -0.68^\circ\text{C}$ (development threshold temperature) and $K = 243.9$ day-degrees (thermal constant).

TABLE 1. Observed values of $\text{FPT}(\Psi)$ and $\overline{\text{FT}}(\Psi)$ (in larvae per female) and of $D_{50\%}(\theta)$ and $\overline{D}_{50\%}(\theta)$ (in days). N is the number of observed aphids and θ is the temperature.

θ (°C)	N	$\text{FPT}(\Psi)$	$\overline{\text{FT}}(\Psi)$	$D_{50\%}(\theta)$	$\overline{D}_{50\%}(\theta)$
10	82	66.5	60.6	21	19
15	105	70.6	68.1	16	15
20	65	53.3	48.0	13	11
25	62	46.2	44.9	9	9

Parameter estimation

A, K and B parameters [equation (15)] were estimated by using the GaussMarquardt non-linear least square method (Marquardt, 1963), performed with the NONLIN procedure of SAS software (SAS Institute Inc., 1988).

Experimental data

Observations were performed under controlled conditions in a programmable heating-cooling apparatus provided with a lighting system giving a light density of about 4,000 lux at 50 cm from light source and composed of two 20 W neon tubes ("cool white" model). Aphids were placed on wheat (cv. Arminda) seedling plants at the four-leaf stage. Wheat was cultivated in black plastic pots using an equal mixture of compost and sand. Each experimental unit was enclosed individually in a perforated cellophane bag, to allow good ventilation. Plants were renewed regularly to ensure a good nutritional value. Experiments were performed at four temperatures (10°C, 15°C, 20°C and 25°C) and with one photoperiod of 16 h. Approximately 100 first instar larvae born of alates were issued from three different clones and produced in standard conditions (20°C, 16 h). Individually, they were placed on seedling plants and observed every day. The date of adult moult and the daily fecundity were recorded.

In addition, data from similar experiments performed by J.-C. Simon and collaborators (in prep.) were used in order to obtain more general results. Reference is also made to another set of data based on embryo counting by adult dissection (Caillaud et al., 1994).

RESULTS AND DISCUSSION

The estimates of A, B and K are given in Table 2. Figs 1 to 4 show model estimations in comparison with the observed data. Often, the model is slightly biased. This is particularly true under low temperature conditions. At 15°C, fecundity is underestimated between the twentieth and the fortieth days, and then it is overestimated towards the end of the reproductive period. In our model, ovulation activity continued throughout adult life. However, from a given age, the decrease in aphid metabolic efficiency and expected life duration

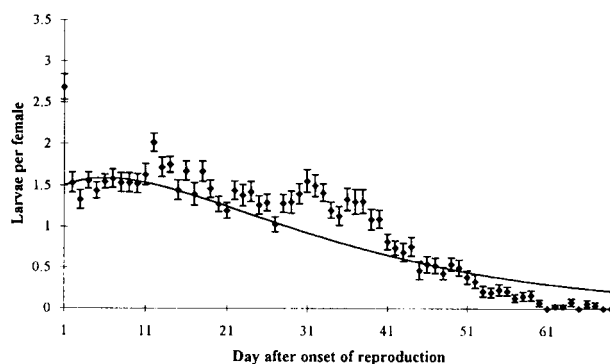


Fig. 1. Comparison between observed (with standard error) and estimated reproduction rate (in larvae per female per day) under constant temperature regime of 10°C (N = 82).

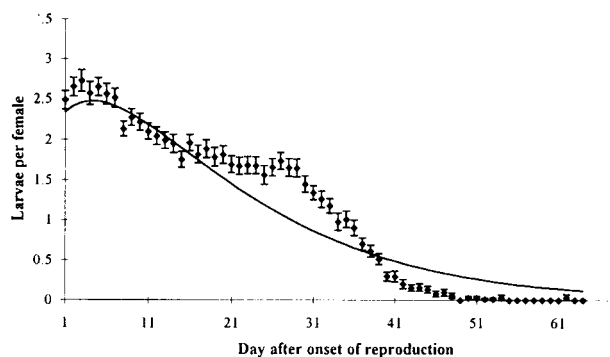


Fig. 2. Comparison between observed (with standard error) and estimated reproduction rate (in larvae per female per day) under constant temperature regime of 15°C (N = 105).

in number of embryos present in ovarioles throughout adult life. Moreover, it would not substantially increase the accuracy of the overall model as, in terms of aphid population dynamics, as seen in similar organisms according to their reproduction characteristics, the sensitivity of models to errors on fecundity parameter estimates shows a strong decrease with female age, the last-born larvae contributing very little to the intrinsic rate of population increase (Wyatt & White, 1977).

makes the continuation of ovulation activity unfavourable. From that age onwards, most of the acquired energy is devoted to the growth of the more developed embryos (Dixon et al., 1993) and, as a consequence, the hypothesis of embryo age structure stability becomes inaccurate. Since our model underestimates the number of embryos that have reached maturity, the larvae laying rate is also underestimated, resulting in an excess of larvae laying compared with the prediction provided by the theoretical curve. The deficit noticed in experimental data after the fortieth day is a result of the rapid decline in embryo numbers due to the early termination of ovulation activity. Therefore, it would be necessary to condition the ovulation rate via adult survival probability. However, such a procedure would greatly complicate the fecundity function and would require an accurate observation of the changes

TABLE 2. Results of A, B, and K parameters estimation.

Parameters	A	B	K
Estimated value	1.34	1.46	1.10
Asymptotic confidence interval (p = 0.95)	1.26–1.43	1.37–1.56	1.03–1.16
Asymptotic correlation	A–B	A–K	B–K
	–0.95	0.78	–0.86

Comparison between estimated $r(\cdot)$ function and dissection data

Let $Bt(x) = n(x) + \beta(x)$ (number of larvae already produced + number of embryos present, at age x). At any age x ,

$$Bt(x) = \beta(0) + \int_0^x r(u) du = \beta(0) + \int_0^x \frac{A \cdot FPT(\psi)}{u+B} \cdot e^{-K \cdot u} du \quad (19).$$

This quantity may be calculated from the estimation of parameters A , B and K , by means of numerical integration using MATHEMATICA software (Wolfram, 1992).

Caillaud et al. (1994) performed dissections with embryo counting on grain aphids cultured at 20°C, under the same conditions as the present study and at three different dates (t_0 , $t_0 + 7$ days, $t_0 + 10$ days). These experiments provided an estimate of the actual value of $Bt(x)$ for each of the three dates ($x = 0$, $x \approx 0.59$ and $x \approx 0.85$). Fig. 5 presents model estimations compared with observed values of $Bt(x)$. Although the amount of newly ovulated embryos after adult moult is actually less than the model prediction, it is of the same order of magnitude. We consider this discrepancy to have the same source as that discussed above.

Caillaud et al. (1994) observed an average achieved fecundity (56.4 larvae per females),

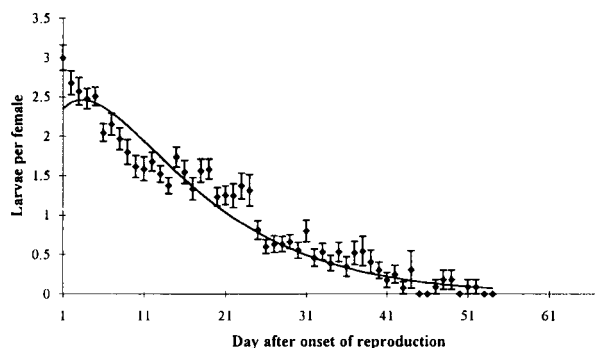


Fig. 3. Comparison between observed (with standard error) and estimated reproduction rate (in larvae per female per day) under constant temperature regime of 20°C ($N = 65$).

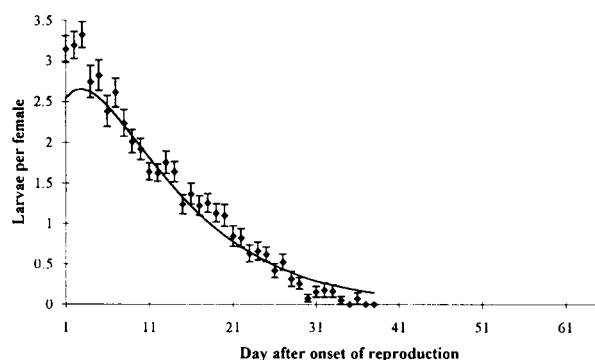


Fig. 4. Comparison between observed (with standard error) and estimated reproduction rate (in larvae per female per day) under constant temperature regime of 25°C ($N = 62$).

which was less than the total number of embryos present at the time of adult moult. Adults should then increase the rate of development of already-formed embryos, rather than invest a proportion of their acquired energy in producing new embryos that risk not achieving full growth. The contradiction to data implies the existence of a constraint restricting the embryos growth rate, which confirms Kindlmann and Dixon's hypothesis. In the same way, unless females die with ovarioles filled with immature embryos (at day 10, the value of $Bt(x)$ reaches 73.4 larvae per female, i.e., 17 larvae in excess to the average total amount of larvae produced), some embryos are resorbed in the second part of the reproductive period, thus allowing females to maintain a high fecundity despite the decline of their metabolic efficiency. Thus, embryos produced by ovulation after adult moult may be

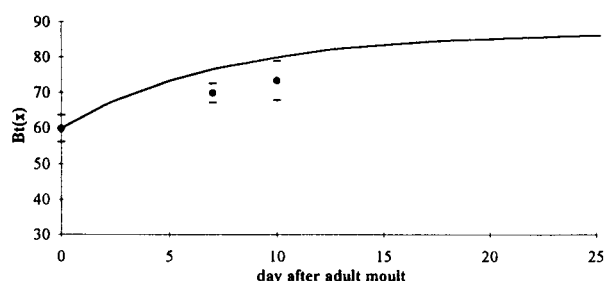


Fig. 5. $Bt(x)$ evolution observed (from Caillaud et al., 1994) and predicted by the model.

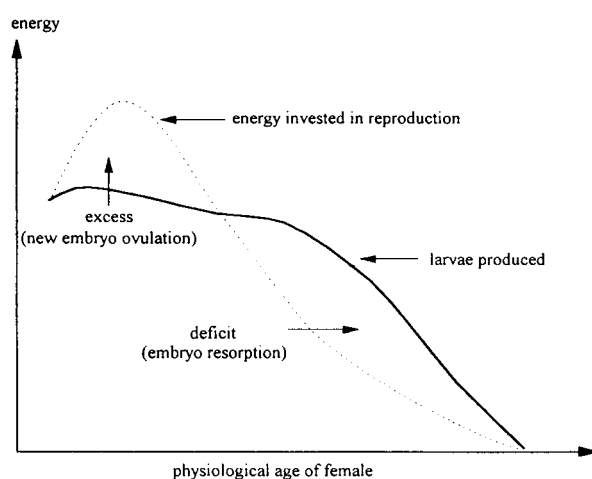


Fig. 6. Schematic diagram of assumed gonad functioning in *Sitobion avenae*.

considered as a reserve organ (Fig. 6), which contributes to the bias discussed in previous sections.

CONCLUSIONS

The present model, unlike most others, takes temperature into account. Moreover, it introduces ageing rate of adults, ovulation rate and total potential fecundity, the variability, heritability or susceptibility to environmental factors of which can be studied by means of simulations. However, this work does not focus on physiological aspects and some biases remain due to complex phenomena (resorption).

We attempted to construct a theoretical framework for interpreting the specific characteristics of grain aphid (*Sitobion avenae*) reproduction by adjusting the theory proposed by Kindlmann & Dixon (1989).

However, some gaps in our knowledge remain, particularly with respect to the environ-

mental or/and intrinsic controls over total amount of reproduction in the clones studied. In particular, the relation between potential fecundity of aphids and phenological stage of the host-plant appears to be very important for aphid population dynamics in the field and requires additional study.

The approximate triangular fecundity function is typical for most insect species. The ovulation pattern is also fairly general. The model itself uses the grain aphid as a model species, but its framework may be applied to other insect species. If empirical data are available, the proper form of the $r(\cdot)$ function may be estimated, which then implies the shape of the fecundity function.

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