Models of sexual and asexual coexistence in aphids based on constraints


Laboratoire de Zoologie, INRA, Domaine de la Motte-au-Vicomte, F-35653 Le Rheu cedex, France, e-mail: rispe@roazhon.inra.fr
Laboratoire d'Evolution et Systématique des Végétaux, Université de Paris-XI, Bât. 362, F-91405 Orsay, France

Key words: Sex; parthenogenesis; constraint; ESS; aphids.

Abstract

Two models are presented to test the hypothesis that in aphids, a particular constraint (the necessity to resist frost) could be the proximal cause for the maintenance of sex. Both models are based on temporal variability in winter survival of asexuals.

They show that:
1) only cyclical parthenogenesis is maintained below a threshold frequency of mild winters, because of the cold-resistance of sexually-produced eggs.
2) above a second threshold, only obligate parthenogenesis is maintained.
3) in-between, the first model predicts a mixed evolutionarily stable strategy (ESS). This would reflect well the geographic distribution of the different types of reproduction. The second model, based on the genetic control of the reproduction system in two aphid species, predicts the maintenance of polymorphism with fluctuating proportions of the two life-cycles. Males produced by obligate parthenogens play an essential role in this equilibrium (no stable polymorphism exists if this male production is set to zero). The value of the lowest possible fitness achieved by overwintering asexuals is critical.

Introduction

The prevalence of sexual reproduction among extant species in spite of the cost of producing males remains an unexplained paradox. This reproductive cost is twofold in anisogamous sexual populations with a balanced sex ratio (Maynard Smith, 1971), which should lead to the rapid displacement of sex in case of competition with asexual lineages. The well-known long-term advantages of sex,
which are the faster combination of favourable mutations (Muller, 1932) and the
avoidance of the accumulation of deleterious mutations (Muller, 1964), are clearly
not sufficient to explain its short term maintenance. This led Williams (1975) to
postulate that there should be some immediate advantage to sex that should more
than compensate this cost. This "balance argument" has inspired many models
based on a presumably universal short-term advantage of sex.

One of the first was Williams and Mitton’s aphid-rotifer model (Williams and
Mitton, 1973), based on the idea of a "genetic lottery". In a heterogeneous and
unpredictable environment, with intense sib-competition, sex could be periodically
advantageous as it allows maximising the chances of producing locally fittest
genotypes. Most of the subsequent models were also based on the advantage of
producing genetically more diverse offspring, a consequence of recombination (for
a review, see Michod and Levin, 1988 and Stearns, 1990). This also applies to the
trendy "Red Queen" hypothesis (Van Valen, 1973) which emphasises the necessity
to evolve fast in a fast-evolving environment. For example, the pressure represented
by parasites which cause a frequency-dependent selection in the host could promote
sex as a means to produce variable and new genotypes with higher fitness
(Hamilton, 1980). More recently, it has been shown that combinations of effects,
such as selection against mutation accumulation and host-parasite coevolution
(Howard and Lively, 1994), or beneficial and deleterious mutations (Peck, 1994)
may provide plausible conditions for the maintenance of sex in the short term.

Species where sexual and asexual lineages coexist offer a special interest when
trying to identify the selective forces responsible for the maintenance of sexuality.
Some studies of such organisms seemed to have backed up the hypothesis of an
advantage of sex due to diversity in the context of parasitism, for example in snails
(Lively, 1992) and fishes (Lively et al., 1992). But many other examples suggest a
different proximal cause for the maintenance of sex, as it is the case whenever there
is a link between sexual reproduction and an ecological function (Lloyd, 1980). In
aphids, for example, sex is the only means to produce a cold-resistant form, the
eggs (Remaudière, 1953; Leather, 1992). The necessity to resist cold would thus
provide a constraint on the maintenance of sex, regardless of the genetic diversity
it provides.

We present in this paper two models based on the hypothesis of a short-term
advantage of sex due to its ecological advantage instead of genetic diversity in
aphids. The basic ingredient of the models is temporal variability of winter survival
of asexuals. Asexuals readily achieve reproduction during mild winters and get a
much higher fitness that sexuals, but have a low survival in cold winters. We
examine the range of fluctuating selection that permits the maintenance of both
modes of reproduction. The first model is phenotypic and assumes that mixed
strategies (between asexual and sexual) may be achieved. Intermediate strategies
(life-cycles) have been found in some clones of a number of aphid species, including
Acrystosiphon pisum (Mackay, 1989), Megoura viciae (Lees, 1959), Sitobion avenae
(Wegorek and Dedryver, 1987), and Rhopalosiphum padi (Tatchell and Parker,
1990); in conditions including the production of sexuals, theses clones keep produc-
ing both sexual and parthenogenetic females. The second model incorporates
experimental knowledge of the genetic determinism of life-cycle in two aphid species; an important feature is that it considers the possibility for normally asexual lineages to produce a small number of males, which is frequent in aphids and daphnia but has received little attention from modellers, although the balance between sexuals and asexuals is very likely to be affected by this phenomenon.

Models

1. The “gambler/saver” phenotypic model

In this model, we consider cyclical and obligate parthenogenesis as two alternative strategies in competition within a population. Cyclical parthenogens have a low reproduction rate through the winter, but play it safe because they produce cold resistant eggs. Conversely, obligate parthenogens might exhibit relatively high reproductive success after a mild winter but suffer high mortality during a cold winter. An analogy may thus be found in the comparison between a saver and a gambler (the former seeks security while the latter might either win a lot more or lose his entire stake).

We assume that there are two types of winter, “mild” and “cold”, and define the probability of occurrence of a mild winter ($p$). Table 1 indicates the multiplicative coefficients used to evaluate the relative success of either strategy after a cold or a mild winter. Cyclical parthenogens are assumed to get a constant winter fitness (1), while the winter fitness of obligate parthenogens is either much higher ($G$) – in mild winters – or much lower ($c$) – in cold winters. We try to identify an evolutionarily stable strategy (ESS) between the different reproductive strategies (Maynard Smith, 1982) assuming that any mixed strategy is possible and using analytical methods. A given strategy is characterised by the ratio $\alpha$ of obligate parthenogens (ratio of gamblers) produced in the autumn (Fig. 1). With $W(\alpha, z^*)$ being the relative fitness of the strategy $\alpha$ in a population that has adopted the strategy $z^*$, there are two possible issues:

<table>
<thead>
<tr>
<th>Type of winter</th>
<th>Mild</th>
<th>Cold</th>
</tr>
</thead>
<tbody>
<tr>
<td>Obligate parthenogenesis (gambler)</td>
<td>$G \gg 1$</td>
<td>$c \ll 1$</td>
</tr>
<tr>
<td>Cyclical parthenogenesis (saver)</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>
Fig. 1. Definition of a mixt strategy in the phenotypic model. It is characterised by the rate $x$ of parthenogens versus $1 - x$ of sexuals produced in the autumn.

after a cold winter:

$$W(x, x^*) = \frac{xG + 1 - x}{x^*G + 1 - x^*} \quad (1)$$

after a mild winter:

$$W(x, x^*) = \frac{xG + 1 - x}{x^*G + 1 - x^*} \quad (2)$$

So on average:

$$\bar{W}(x, x^*) = (1 - p) \frac{xG + 1 - x}{x^*G + 1 - x^*} + p \frac{xG + 1 - x}{x^*G + 1 - x^*}. \quad (3)$$

We first check whether $x^* = 0$ (100% cyclical parthenogenesis) or $x^* = 1$ (100% obligate parthenogenesis) may be an ESS:

if $c^* = 0$, $W(x^*, x^*) = 1$ and $W(x, x^*) = 1 + x[pG + (1 - p)c - 1]$.

It is an ESS if $\bar{W}(x^*, x^*) > W(x, x^*)$ whatever $x$, so if $pG + (1 - p)c < 1$ (condition 1).

If $x^* = 1$, $\bar{W}(x^*, x^*) = 1$ and $W(x, x^*) = p\frac{1}{G} + (1 - p)\frac{1}{c}$

$$+ x \left[ 1 - p \frac{1}{G} - (1 - p)\frac{1}{c} \right].$$

It is an ESS if $\bar{W}(x^*, x^*) > W(x, x^*)$ whatever $x$, so if $p < 1/G + (1 - p)/c < 1$ (condition 2). Note that in the case where $c = 0$ (null survival of obligate parthenogens in cold winters) then $x^* = 1$ can never be an ESS, except if $p = 1$, i.e. if cold winters never occur.

For other values of $x^*$, we seek values of $x$ where $d\bar{W}/dx = 0$. The solution obtained is
Models of sexual and asexual coexistence in aphids

\[ x^* = \frac{pG + (1 - p)e - 1}{G + e - Ge - 1} \]  \hspace{1cm} (4)

For this value of \( x^* \), we have for all \( x \): \( \bar{W}(x, x^*) = \bar{W}(x^*, x^*) \). Thus, \( x^* \) is an ESS only if \( \bar{W}(x^*, x) - \bar{W}(x, x) > 0 \) when \( x \neq x^* \). We show that this is always the case when none of the two previous conditions is true (Appendix 1) and, therefore, that the value given by Eq. 4 is an ESS.

To summarise, if the condition 1 is met (if \( p \) is lower than a first threshold), the ESS is \( x^* = 0 \) or 100% cyclical parthenogenesis; if the condition 2 is met (if \( p \) is higher than a second threshold), the ESS is \( x^* = 1 \) or 100% obligate parthenogenesis. If none of these conditions are met (for intermediary values of \( p \)), there is a mixed ESS (Eq. 4), and therefore a mixture of cyclical and obligate parthenogens.

Finally, we show in Appendix 2 that the ESS calculated above is the strategy that maximises the geometric mean fitness, which is a more classical approach to problems of selection fluctuating in time. Both methods are equivalent and yield the same result.

2. Model specifying the genetic determination of cycle and sex ratio

Biological data on the genetic determination of life-cycle in aphids

The genetic basis of the different types of life-cycle has been extensively studied in two aphid species, *Myzus persicae* (Blackman, 1972) and *Rhopalosiphum padi* (Simon, 1991; Simon et al., 1994). A single locus appears to determine the type of reproduction, cyclical parthenogenesis being dominant over obligate parthenogenesis. Although intermediary clones have also been found in *R. padi* as mentioned above (Tatchell and Parker, 1990), they appear to be a small minority and are not taken into account in this model; we thus only consider the two fundamental types of clones in these species (Fig. 2), clones retaining the ability to produce both kinds of sexuals and clones that lose this ability. Cyclically parthenogenetic clones in these species present a pattern of sexual progeny production which is typical of host-alternating aphids, with the production of gynoparae (special parthenogenetic females that produce sexual females) and males in the autumn (Dixon and Glen, 1971). For the sake of clarity, gynoparae are not referred to here as “parthenogenetic females”, the latter term being applied only to parthenogenetic females that produce other parthenogenetic females. Obligately parthenogenetic clones, which reproduce by continuous parthenogenesis, often retain the ability to produce some males.

Hypothesis on the genetic determination

We adopt the hypothesis of a single locus gene determining the type of reproduction, cyclical parthenogenesis being dominant and (male-producing) obligate parthenogenesis being recessive. Because of its theoretical interest, we also examined the reverse hypothesis, considering obligate parthenogenesis dominant. Furthermore, the sex ratio is also assumed to be genetically determined by a second
Fig. 2. Parameters of a genetic model of selection between two types of life-cycles in an aphid species, *R. padi*. The gynoparae are special parthenogenetic females which give birth to sexual females. Obligate parthenogens produce males (the case of no male-production is also examined). The rate of males, $S$, depends on the sex ratio genotype. The multiplicative winter fitness of a gynopara is $I$ while the fitness of parthenogenetic overwintering is $G$ after a mild winter and $\epsilon$ after a cold winter.

## Table 2. Proportion of males depending on the sex ratio genotype.

<table>
<thead>
<tr>
<th>Sex ratio genotype</th>
<th>$A_1A_1$</th>
<th>$A_1A_2$</th>
<th>$A_2A_1$</th>
<th>$A_2A_2$</th>
<th>$A_2A_3$</th>
<th>$A_3A_3$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion of males</td>
<td>0.80</td>
<td>0.65</td>
<td>0.50</td>
<td>0.50</td>
<td>0.35</td>
<td>0.20</td>
</tr>
</tbody>
</table>
Models of sexual and asexual coexistence in aphids

Principles of the simulation

The simulation is carried out as follows: successive winters are randomly "cold" or "mild" (the average proportion of mild winters being \( p \)) as in the preceding model. The genotypes of cyclical parthenogens (MM or Mm) are generated only by sexuality while genotypes of obligate parthenogens (mm) can be generated as a result of both ways of overwintering: parthenogenetically, with the progeny of the parthenogenetic females produced in the autumn, and sexually, because this trait is recessive and segregation in the sexual process can give rise to offspring carrying the homozygous recessive genotype.

In the alternative hypothesis (obligate parthenogenesis dominant), sexual reproduction can only generate cyclical parthenogens (MM) and obligate parthenogens that are heterozygotes (Mm), never homozygotes.

The parameters giving the successes of the different overwintering strategies \((G, c, p)\) are similar to the ones used in the gambler-saver model.

To determine the frequencies of genotypes arising from sexual reproduction, we assume that mating is random, and that there is no migration. The sex ratio and type of life-cycle loci are assumed to be independent, while the population size is held constant.

We assume the type of life-cycle is selectively neutral during the summer, an assumption that appears justified by experimental comparison of the intrinsic rates of increase of different types of clones (Rispe et al., 1996). Therefore, the frequencies of the different genotypes in spring remain unchanged until the next sexual process.

Starting with equal frequencies of all genotypes, the process is repeated for several years. It is then possible to monitor the frequencies of the genotypes in the generation preceding the production of gynoparae and males, and consequently the relative abundance of gynoparae, males and parthenogenetic females.

We first present general results of the model for variable values of the asexuals' winter fitness \((G\) or \(c\)) in each situation: cyclical parthenogenesis dominant or recessive, male- or non-male-producing obligate parthenogens. Then we examine a particular situation leading to polymorphism for life-cycle and sex ratio. Finally, we compare the mean proportions of parthenogenetic females in the genetic model (with different assumptions) with the proportion of obligate parthenogens which is an ESS in the first model, in two particular situations - \( G = 4 \) and \( c = 0.1 \) or \( c = 0 \). These situations were chosen as being representative of a variable winter climate, which would be either mild (and give a substantial advantage to asexual overwintering) or cold (with either low or null fitness for asexuals).

The program was written in PASCAL (TURBO PASCAL release) and run on an IBM-PC computer.

General results

We found that when the highest fitness achieved by overwintering asexuals \((G)\) is lower than half that of a sexual female \((l)\), obligate parthenogens (the \( m \) allele) are always eliminated. Conversely, when the lowest fitness achieved by overwintering asexuals \((c)\) is greater than half that of a sexual female, cyclical parthenogens (the
Fig. 3. Results of simulations of the genetic model when obligate parthenogens do (upper part of the graph) or do not produce males (lower part), for $G > 0.5$ and $\varepsilon < 0.5$ (and $\epsilon \neq 0$), depending on the probability of a mild winter ($p$). The figure indicates the allele(s) maintained at the life-cycle locus (M/m) and at the sex ratio locus (A1/A2/A3).

M alleles are always eliminated. This reflects the cost of producing 50% males in the sexual generation of cyclical parthenogens. This cost is compensated when sexual females are at least twice as fit as asexual females. Therefore, if $\varepsilon > 0.5$, the twofold cost of male-production is never compensated and cyclical parthenogens are eliminated. If $G < 0.5$, the cost of males is always compensated; sexual reproductions is always at an advantage, and obligate parthenogens are eliminated.

In all other cases (when $G > 0.5$ and $\varepsilon < 0.5$), the result depends on the proportion of mild winters, $p$. When no males are produced by obligate parthenogens, only two situations are found: below a threshold value of $p$, only cyclical parthenogens (M) remain, while above this threshold, only obligate parthenogens (m) remain (Fig. 3).

With a male-production in obligate parthenogens (cyclical parthenogenesis being dominant or recessive), three situations can be found if $\epsilon > 0$, as in the ESS model (Fig. 3): below a threshold frequency of mild winters ($p$), only the allele of cyclical parthenogenesis (M) does persist in the long run. The population retains a polymorphism for sex ratio (A1, A2 and A3 are maintained) and produces 50% of gynoparae and 50% of males every autumn. Above a second threshold frequency of mild winters, only the allele of obligate parthenogenesis (m) is maintained. The
allele giving the highest rate of parthenogenetic females ($A_1$) is selected, while $A_2$ and $A_3$ are eliminated. Between the two thresholds, polymorphism for life-cycle is protected. Both $M$ and $m$ are maintained in the long run. For the sex ratio gene, the allele corresponding to the highest rate of males ($A_1$) is always eliminated. Both $A_2$ and $A_3$ are maintained for low values of $p$, while only $A_1$ is maintained for higher values.

For $\varepsilon = 0$, obligate parthenogenesis cannot invade except when $p = 1$ (null probability of a cold winter). When the survival of overwintering parthenogens is null, the protection of the $m$ allele strictly depends on the maintenance of cyclical parthenogens and is therefore conditioned to the maintenance of the $M$ allele.

**Detail of a particular situation leading to polymorphism**

For $G = 4$, $c = 0.1$ and $p = 0.30$, with cyclical parthenogenesis dominant, a dynamic balance is observed in the long run between the different life-cycle alleles. After a succession of mild winters, the proportion of parthenogenetic females ($P$) increases up to a maximum (0.80) whereas it becomes nearly zero after a succession of cold winters (Fig. 4). Meanwhile, an approximate equilibrium is maintained between gynoparce (G) and males (M), due to selection for a balanced sex ratio. The frequencies do not stabilise, because of the fluctuating winter-conditions, but

![Fig. 4. Simulated frequencies of the different morphs produced in the autumn in the aphid R. padi: parthenogenetic females, gynoparae and males. Each point represents the frequencies of the three morphs in a given autumn, the simulation being carried out over 2500 years. With $p = 0.30$, $G = 4$ and $\varepsilon = 0.1$.](image-url)
the mean frequencies (mean of the frequencies from the beginning of the simulation) converge towards intermediate values, which, in this case, are $P = 0.316$, $G = 0.335$, and $M = 0.348$. The sex ratio alleles $A_3$ and $A_4$ are maintained while $A_1$ is eliminated. Therefore the proportion of males is constrained between 50% (when $A_3$ is near fixation) and 20% (when $A_4$ is near fixation).

Comparison between the "gambler-saver" and the genetic model under different assumptions

Finally, a comparison is made (Fig. 5) between the average frequencies of parthenogenetic females ($P$, curves A, B, C) found in the genetic model under different assumptions, and the optimal proportion of obligate parthenogens ($x^*$, curve D) calculated in the gambler-saver model, under different climatic conditions (different values of $p$), for $G = 4$ and $\varepsilon = 0.1$ (Fig. 5a) or $\varepsilon = 0$ (Fig. 5b).

The comparison between curves A (male-producing obligate parthenogens) and B (non-male-producing obligate parthenogens) – both with cyclical parthenogenesis dominant – shows the dramatic effect of male production by obligate parthenogens. It leads to polymorphism where there would be none otherwise. Specifically, polymorphism appears where only cyclical parthenogens would persist otherwise (Figs. 3 and 5); this character is then advantageous to obligate parthenogenesis genes. It is mostly evident in the case $\varepsilon = 0$, i.e. when cold winters are lethal for overwintering asexuals: polymorphism is still maintained for high probabilities of cold winters if males are produced by obligate parthenogens, whereas obligate parthenogens are systematically eliminated otherwise (except when $p = 1$, when there are never cold winters). For $\varepsilon = 0.1$, obligate parthenogens invade above the same threshold value of $p$ in either case (with or without male production by mm).

When cyclical parthenogenesis is recessive (curve C), obligate parthenogens invade above the same threshold value of $p$ as when cyclical parthenogenesis is dominant. But polymorphism appears only for higher values of $p$, and the average proportion of (winter) parthenogenetic females remains lower (compare curves A and B). This may be explained by the fact that when obligate parthenogenesis genes are dominant, they are more exposed to selection: a single cold winter will eliminate most $m$ alleles of the population. In addition, sexual reproduction will never give birth to homozygotic obligate parthenogens, only to heterozygotes.

The ESS ($x^*$) and the average proportion of parthenogenetic females in the genetic model $P$ (assuming male production in obligate parthenogens), are very close when $\varepsilon = 0$ (compare curve D with A and B). In all cases (A, B, C, D), obligate parthenogens never invade, except for $p = 1$ (no cold winters). The shape of the curve for the genetic model (A and B) is approximately linear up to a certain point, where it reaches a maximum governed by the assumed constraints introduced by the genetic determination of sex ratio. Since the minimal rate of males is fixed at $S = 0.20$, the ratio of parthenogenetic females cannot exceed 0.80. If we assume that phenotype $S = 0$ is displayed by one sex ratio genotype ($A_3A_3$ for example), the results of the genetic model fit better with the gambler-saver model even for high values of $p$ ($P$ then tends towards unity).
Fig. 5. a and b. Comparison between the ESS model and the mean proportions of parthenogenetic females (P) in the genetic model under different assumptions, with $G = 4$ and $\varepsilon = 0.1$ (Fig. 5a, upper graph) or $\varepsilon = 0$ (Fig. 5b, lower graph), for different values of the proportion of mild winters ($p$, x-axis). For the genetic model (curves A, B, C), the figure indicates average proportions of parthenogenetic females after simulating a succession of 50,000 years (A, C) or $10^6$ years (B). A – cyclical parthenogenesis dominant, male-producing obligate parthenogens. B – cyclical parthenogenesis dominant, non-male-producing obligate parthenogens. C – cyclical parthenogenesis recessive, male-producing obligate parthenogens. D – ESS ($\alpha^*$) in the “gambler-saver” model.
For $\varepsilon = 0.1$ (Fig. 5b), obligate parthenogens invade above a much lower threshold value of the proportion of mild winters in the genetic model (curves A, B, C) than in the phenotypic model (curve D). A low but non-zero fitness achieved by overwintering parthenogens during cold winters is thus much more critical in the genetic than in the phenotypic model. This can be seen by the fact that curve D (the ESS) changes little between the cases $\varepsilon = 0.1$ (Fig. 5a) and $\varepsilon = 0$ (Fig. 5b) while curves A, B, and C (genetic model) are dramatically displaced to the left when $\varepsilon = 0.1$.

Discussion

The ESS model predicts a stable mixed strategy between cyclical and obligate parthenogenesis in intermediate selection conditions, pure cyclical parthenogenesis in usually cold climates, and pure obligate parthenogenesis in usually mild climates. This model is comparable to models of seed dormancy (Cohen, 1966; León, 1993) where two alternative germination strategies in a fluctuating environment are compared. We found the same conditions for the evolutionary maintenance of the two strategies, i.e. that the arithmetic mean of the (relative) fitness coefficient of the variable strategy must be superior to unity (condition 1) and that the arithmetic mean of the inverse of this coefficient must also be superior to unity (condition 2). In addition, here we calculated the intermediary ESS between the two alternative strategies when both conditions are met.

The genetic model predicts an unstable polymorphism in intermediary selective conditions, and shows an increased realism compared with the phenotypic model, since it takes into account the production of males by obligate parthenogens. These males play a crucial role in the equilibrium between the two reproductive strategies, carrying the allele of obligate parthenogenesis (m) into the sexual process. By the way, this allele benefits from the shelter of the cold resistant eggs, which is critical during cold winters. As a consequence, this leads to polymorphism in conditions where only cyclical parthenogens would persist otherwise. The same conclusion holds with the hypothesis that cyclical parthenogenesis is dominant or recessive, the latter case leading to lower frequencies of (winter) parthenogenetic females on average, and thus being less advantageous to obligate parthenogenesis.

This model also shows that the value of the minimal survival rate of overwintering parthenogens ($\varepsilon$) is critical: when this value is null, obligate parthenogenesis can never invade, while it invades above a rather low threshold of the frequency of mild winters if it is only small. This model falls within the general framework described by Haldane and Jayakar (1963); the balance between cyclical and obligate parthenogenesis in aphids appears therefore as a particular case of the maintenance of polymorphism under fluctuating selection.

The cold resistance of sexually produced eggs is sufficient to explain the geographic distribution of life-cycles in many aphid species (Lees, 1966; Blackman, 1981). In aphids, where obligately parthenogenetic lineages and cyclically parthenogenetic lineages may coexist, there is a well-established correlation between the
Models of sexual and asexual coexistence in aphids

 proportion of cyclical parthenogens and latitude (i.e. the winter severity). This is the case for *M. persicae* (Blackman, 1972), *Metopolophium dirhodum* (Dean, 1974), * Macrosiphum rosae* (Wohrmann and Tomiuk, 1988), *A. pisum* (Mackay et al., 1993), *Schizaphis graminum* (Daniels, 1956; Puterka and Peters, 1990) and *R. padi* (Dedryver, 1983, Tatchell et al., 1988). In addition, there is a strong tendency in tropical aphids species to become obligately parthenogenetic (Moran, 1992); it is also remarkable that root aphids often tend to be obligate parthenogens, which may be related to their inhabiting in a buffered environment where the risk of lethal cold temperatures is lower. A further example may be that of the species of the tribe Tramini which live in ant nests (Moran, 1992) and where sex is abandoned. In Adelgidae and Phylloxeridae, parthenogenetic reproduction is oviparous, which means that sex is not the only way to produce eggs. It seems at least in Adelgidae that there is a greater occurrence of obligate parthenogenesis (Hebert, 1987), which may be explained by the fact that the constraint favouring sex in other aphids is relieved, and that nothing prevents these species from becoming asexual.

The model proposed by Williams and Mitton (1973) does not explain the geographic distribution of sex in aphids in relation to climate. Nor does it explain directly the link between the period of sexual reproduction and environmental determinants (aphids reproduce sexually just before winters), though these authors have argued that the optimal timing for sex would occur for the generation encountering the least predictable conditions. In addition, this model is based on the assumption of intense competition between sibs which is unlikely to be met in many of these species. There are certainly other factors that could play a role in the selection of sex in aphids, but the most parsimonious explanation seems to be based on its link with an ecological function. In many other species, a similar constraint could provide a short-term reason for the maintenance of sex; in rotifers, sex is the only means by which resistant forms can be produced. The same applies to plants in which sexually produced seeds represent both the resistant form and the only efficient system of dispersal. In daphnia, the resistant form to drought, the ephippium, is generally produced sexually, although a few species seem to be able to produce ephippia asexually (Hebert, 1981). Two of these species (*Daphnia cephalata* and *D. middendorffiana*) are entirely asexual, which suggests that sex is maintained only when it confers an ecological advantage. In each of these examples, the proximal cause for the maintenance of sex could then be specific. This suggests that there may be no absolutely unique and universal short-term advantage of sex, but a broad array of specific advantages, often linked to specific constraints. Long term selection at the species level would sort out species that have remained sexual for whatever short-term reason (Nunney, 1989, Gouyon et al., 1989), because they retain greater evolutionary capacities.

The models presented in this paper are based on simplified assumptions, and in particular do not take into account the possibility of migration. However, aphids are able to fly long distances, which is likely to modify the proportions of the different reproductive strategies in a given region (Smith and MacKay, 1989). Cold regions where cyclical parthenogenesis is selected could be regularly provided with migrants from milder regions and from obligately parthenogenetic clones. Con-
versely, cold regions could provide mild regions with cyclically parthenogenetic clones. The equilibrium between the different reproductive strategies under a given climate (and given selection condition) might then be altered by the intensity and direction of migration.

New methods of investigation and data analysis should be used to ascertain the gradient of maintenance of sexuality with latitude in aphids:

- the rate of sexual morphs in the suction traps networks can be analysed and linked with the characteristics of the local climates (Rispe et al., 1998). Unfortunately, these studies are restricted by the difficulty of distinguishing the gynoparae in most aphid species.
- genetic markers of the type of life cycle have recently been identified (Simon et al., 1996) and will be used to estimate the ratio between strategies in different populations and assess the level of gene flow between cyclically and obligately parthenogenetic clones.

Acknowledgements

We thank Drs Y. Robert, M. Hullé, C.-A. Dedryver, Joe Peck, Susan Mazer and two anonymous reviewers for their valuable comments and helpful criticisms. This work was supported by a grant of the French Ministère de l’Agriculture (D.G.E.R.) (contrats n°89131 et 93135).

References

Models of sexual and asexual coexistence in aphids


Received 10 March 1997; revised 18 June 1997; accepted 15 August 1997.

Appendices

1. Demonstration that

\[ x^* = \frac{pG + (1 - p)e - 1}{G + e - Ge - 1} \]

is an ESS: We have

\[ Z = E(W(x^*, x) - W(x, x)) = \frac{N}{D}, \]

where

\[ N = \frac{(x^* - x)^2}{(1 - e)(G - 1)} \]

and

\[ D = [x(e - 1) + 1][x(G - 1) + 1]. \]

\( N \) and \( D \) are always positive, so is \( Z \), so

\[ x^* = \frac{pG + (1 - p)e - 1}{G + e - Ge - 1} \]

is an ESS.

2. Demonstration that the ESS is the strategy that maximises the geometric mean fitness. The geometric mean fitness of a mixt strategy \((x \text{ gambler, } 1-x \text{ saver})\) is:
Models of sexual and asexual coexistence in aphids

\[ F(\sigma) = (z - 1 + \sigma)^{1-p} \cdot (zG + 1 - z)^p \]

also written:

\[ F(\sigma) = [z(\sigma - 1) + 1]^{1-p} \cdot [z(G - 1) + 1]^p. \]

The derivative of this function is null at its maximum. We have:

\[
\begin{align*}
\frac{dF(\sigma)}{d\sigma} &= (1-p)(\sigma - 1)[\sigma(\sigma - 1) + 1]^{1-p} \cdot [\sigma(G - 1) + 1]^p + [\sigma(\sigma - 1) + 1]^{1-p} \\
&\quad \cdot p(G-1)[\sigma(G - 1) + 1]^p-1 \\
\frac{dF(\sigma)}{d\sigma} &= \left[\sigma(\sigma - 1) + 1\right]^{1-p} \cdot [\sigma(G - 1) + 1]^p-1 \\
&\quad \times \left[\frac{(1-p)(\sigma - 1)(\sigma(G - 1) + 1) + p(G-1)(\sigma(\sigma - 1) + 1)}{N}\right]
\end{align*}
\]

so

\[
\frac{dF(\sigma)}{d\sigma} = 0 \iff N = 0
\]

\[ N = [(1-p)(\sigma - 1)(\sigma(G - 1) + 1) + p(G-1)(\sigma(\sigma - 1) + 1)] \]

thus:

\[ N = [(\sigma - 1)(\sigma(G - 1) + 1) - p(\sigma - 1)(\sigma(G - 1))] \]

\[ N = 0 \iff \sigma = \frac{(1-p)(\sigma - 1) + p(G - 1)}{(1-\sigma)(G - 1)} = \frac{pG + (1-p)e}{(1-\sigma)(G - 1)} \]

(result identical to Eq. 4).