

Temporal differentiation and spatial coexistence of sexual and facultative asexual lineages of an aphid species at mating sites

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Abstract

Cases of coexisting sexual and asexual relatives are puzzling, as evolutionary theory predicts that competition for the same ecological niches should lead to the exclusion of one or the other population. In the cyclically parthenogenetic aphid, *Rhopalosiphum padi*, sexual and facultative asexual lineages are admixed in space at the time of sexual reproduction. We investigated how the interaction of reproductive mode and environment can lead to temporal niche differentiation. We demonstrated theoretically that differential sensitivity of sexual and facultatively asexual aphids to an environmental parameter (mating host suitability) shapes the two strategies: whereas the sexual lineages switch earlier to the production of sexual forms, the facultative asexual lineages delay and spread out their investment in sexual reproduction. This predicted pattern of niche specialization is in agreement with the temporal structure revealed *in natura* by demographic and genetic data. We propose that partial loss of sex by one pool of aphids and subsequent reduction in gene flow between lineages may favour temporal specialization through disruptive selection.

Introduction

Competition between sexual and asexual relatives must lead either to the extinction of one population or to their segregation (Peck *et al.*, 1998; Doncaster *et al.*, 2000). Whereas asexual populations benefit from a higher multiplication rate, sexual populations have an advantage in heterogeneous environments because of the larger genetic reshuffling caused by sexual reproduction (Peck *et al.*, 1999), which allows sexual populations to develop in a broader array of ecological conditions (Pound *et al.*, 2004). These general predictions are in agreement with the observed geographical patterning of sexual and asexual populations (Vandel, 1928), the latter frequently being restricted to marginal habitats (Peck *et al.*, 1998), such as higher altitudes (Verduijn *et al.*, 2004) or at species range boundaries (Bell, 1982; Lynch, 1984), as

demonstrated in several groups of species (e.g. flatworms, Pongratz *et al.*, 2003; nonmarine ostracods, Horne & Martens, 1999; and apomictic plants, Eckert, 2002; Van Dijk, 2003). In these cases, sexual and asexual relatives do not compete with each other for the same habitats or resources but rather specialize on distinct ecological niches (Smith, 1978; Vrijenhoek, 1984).

Some authors hypothesize that the rare cases of local coexistence of sexual and asexual lineages can be explained by fluctuating environmental conditions (Rispe & Pierre, 1998; Bengtsson & Ceplitis, 2000; Ceplitis, 2001), but the empirical support for this is weak. Here we consider another hypothesis for the local coexistence of reproductive modes: that differential sensitivity to environmental conditions can lead to temporal partitioning of ecological niches within the same site (Hendry & Day, 2005). This was tested on aphids which, like other cyclical parthenogenetic organisms, show numerous examples of stable and even systematic coexistence of sexual and facultative asexual lineages, making them suitable models for investigating the ecology and evolution of sex (Simon *et al.*, 2002;

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De Meester *et al.*, 2004). We extended a previous modelling approach (Halkett *et al.*, 2005a) and made the prediction that sexual and facultative asexual lineages of aphids should differ in their timing of production of sexual forms. In support of this hypothesis, we report the population structure of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), at mating sites, which indicates temporal genetic isolation between reproductive modes.

Materials and methods

The species

In *R. padi*, there are two overwintering strategies associated with reproductive mode variation. Typically, this species alternates several parthenogenetic (clonal) generations (from spring to late summer) and a single sexual one (in autumn), the switch being triggered by decreasing temperature and photoperiod (Dixon & Glen, 1971). Sexual reproduction leads to the production of frost-resistant overwintering eggs. However, complete or partial removal of the sexual phase can occur, resulting in sustained parthenogenetic reproduction throughout the year (Simon *et al.*, 1991). Relative investment in sexual reproduction is expected to be linked to winter severity, which determines the probability of survival of parthenogenetic lineages during winter (Simon *et al.*, 2002). Relative allocation of resources to sexual reproduction dictates the balance between a safe strategy – sexual production of diapausing eggs that survive winter well – and a risky one – parthenogenetic multiplication, which is more efficient (because of a higher population growth rate) but can lead to high mortality in the event of a harsh winter (Rispe & Pierre, 1998; Rispe *et al.*, 1998; Halkett *et al.*, 2004). In Western France, *R. padi* shows local coexistence of sexual and facultative asexual lineages (Delmotte *et al.*, 2002; Halkett *et al.*, 2005a). In autumn, sexual lineages are characterized by a full commitment to sexual reproduction, expressed as an abrupt switch from parthenogenetic reproduction to the production of sexual forms (Simon *et al.*, 1991; Hullé *et al.*, 1999). Alternatively, facultative asexual lineages invest in parthenogenetic and sexual reproduction simultaneously, overwintering consequently both as parthenogenetic forms and frost-resistant eggs, that is, they adopt a ‘bet-hedging’ strategy (Halkett *et al.*, 2004, 2005a) (Fig. 1).

In addition, *R. padi* is a host-alternating aphid, migrating between herbaceous summer hosts (Poaceae) and a woody winter host (*Prunus padus*). The sexual forms (gynoparae – first generation of sexual females – and males) are produced on the summer hosts from which they migrate to their winter host, where sexual reproduction occurs (Dixon, 1971; Fig. 1). Previous studies have suggested that winter unpredictability, the uncertainty of the onset of the period during which the woody host is physiologically suitable for aphids, is an influential

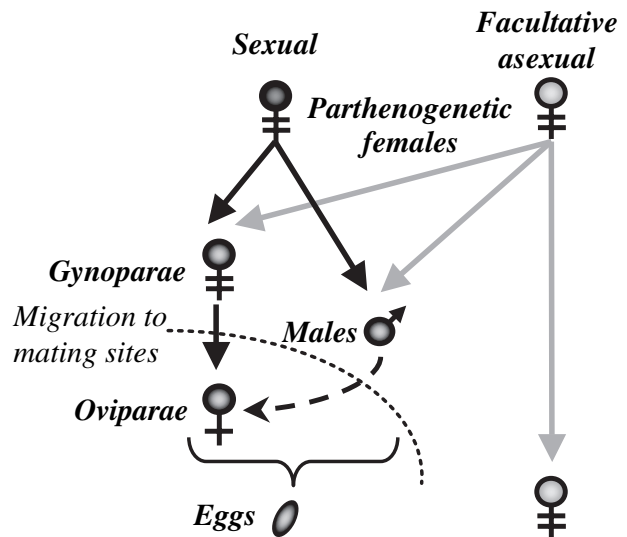


Fig. 1 Schematic representation of the autumnal switch to sexual reproductive mode for the two main reproductive strategies in *R. padi* from Halkett *et al.* (2005a).

ecological factor in the timing of production of sexual forms and hence the dynamics of colonization of mating sites (Ward *et al.*, 1984; Ward & Wellings, 1994; Halkett *et al.*, 2004). Winter unpredictability is determined mainly by climate type (e.g. oceanic vs. continental) and varies in Western Europe from south-west to north-east.

Aphid lineages differing in their reproductive modes also vary with respect to genetic characteristics: whereas aggregations of sexual lineages show little deviation from Hardy–Weinberg equilibrium at highly resolving, selectively neutral genetic markers, populations of facultative asexual lineages show genetic signatures (e.g. heterozygote excess and clonal multicopies), consistent with reproduction being mainly clonal (Delmotte *et al.*, 2002; Halkett *et al.*, 2005a). Therefore, although facultative asexual lineages contribute to the pool of sexual forms at mating sites (Halkett *et al.*, 2005a), they mostly overwinter as parthenogenetic individuals (risky asexual strategy). Moreover, despite the coexistence of reproductive modes, any aphid randomly sampled in the field can be confidently assigned, based on its allelic profile at multiple microsatellite loci, to sexual or facultative asexual populations (Delmotte *et al.*, 2002; Halkett *et al.*, 2005a).

Here, we tested the hypothesis that the maintenance of genetic differentiation despite spatial coexistence results from a prezygotic isolation occurring between sexual and facultative asexual lineages at mating sites. Based on previous knowledge of the sensitivity of aphid populations to winter unpredictability (see below), we investigate how differential responses between sexual and facultative asexual lineages to the same ecological factor

shape different dynamics for the colonization of mating sites.

Theoretical aspects and modelling

In a previous study we developed a theoretical model for predicting the dynamics of the production of sexual forms in response to the level of winter unpredictability (Halkett *et al.*, 2004). In this model, the winter host, where mating occurs, is assumed to be suitable until leaf fall, which is assumed to be the instant of 'arrival of winter'. Winter unpredictability is then modelled as the variance σ in the date of 'arrival of winter'. This model starts with a parthenogenetic female and assumes a constant growth rate (λ) of the population. At each of a finite number of instants (date i), the female has to allocate her total resources between parthenogenetic offspring (proportion β_i) and sexual forms ($1 - \beta_i$). An overwintering strategy (β) is then defined by the vector of the instantaneous proportions (β_i) of parthenogenetic forms produced during time. All the sexual forms produced after the arrival of winter are considered to die without reproducing. The model then calculates the ESS strategy (β^*), which maximizes the fitness of a lineage through its investment in sexual and parthenogenetic reproduction, given the probability distribution of the 'arrival of winter' (σ) – see eqn 3 in Halkett *et al.* (2004).

The simulation results, when σ was varied, showed that when there was great unpredictability in the arrival of winter (such as observed in western France), it paid to delay investment in sexual reproduction and to spread it over the duration of mating host suitability (Halkett *et al.*, 2004). Somewhat paradoxically, this continued investment in sex requires sustaining parthenogenetic reproduction alongside the sexual forms, because sexual reproduction requires parthenogenetic females to produce mating females. This overwintering strategy corresponds to the facultative asexual reproductive mode, which makes the major contribution to the pool of sexual forms in western France (Halkett *et al.*, 2005a). In contrast, the sexual lineages have no option of 'safe' and 'risky' strategies because their total switch to sexual reproduction means the end of parthenogenetic reproduction for that year. Thus sexual lineages concentrate their investment in sexual reproduction into a very short time interval, which is best suited in a more predictable (continental) climate (Papura *et al.*, 2003). The theoretical predictions of this previous model were validated using long time series of aphid catches from various locations in Western Europe, indicating that aphid populations are adapted to the local level of climate unpredictability (Halkett *et al.*, 2004).

The previous model aimed at selecting the best strategy given the local environmental conditions, but could not account for the local coexistence of sexual and facultative asexual lineages, as observed at mating sites (Halkett

et al., 2005a). In particular, it did not allow prediction of the shape of the colonization dynamics of a sexual strategy facing large winter unpredictability. Here we applied the model with the modification that we imposed a constraint on the length of time during which the sexual forms can be produced, to a single date, i . We performed new simulations to compare the optimal response of the constrained (sexual) and unconstrained (facultative asexual) strategies, assuming that they locally coexist, and therefore face the same level of winter unpredictability (σ was set to a large value to mimic oceanic climatic conditions as observed in Western France). We then tested whether the temporal dynamics of sexual forms produced by the sexual and facultative asexual lineages overlap or not. We confronted the predictions of the model with empirical data of the colonization of mating sites (described hereafter).

Monitoring population dynamics and genetics at mating sites

The temporal distribution of sexual and facultative asexual lineages at mating sites was assessed by combining demographic and genetic analyses of populations of sexual forms of *R. padi* sampled on *P. padus*. We first monitored the dynamics of colonization of the sexual forms on *P. padus* trees, as a measure of mating time. Second, as no morphological criteria could distinguish sexual individuals originating from sexual vs. facultative asexual lineages, genetic assignments were performed (see Halkett *et al.*, 2005a for a detailed procedure). We used the STRUCTURE software (Pritchard *et al.*, 2000), which is based on a Bayesian algorithm (Reverse Jump Markov Chain Monte Carlo), to cluster sampled individuals according to their multilocus allelic profile. This individual-based method enables fine-scale temporal structure to be assessed from samples taken during colonization (Hendry & Day, 2005).

Population dynamics

The dynamics of colonization by *R. padi* sexual forms at five mating sites (single *P. padus* trees) located in the same geographical area (5–15 km apart) in western France was monitored in the autumn of 2001. From mid-September to late November (12 weekly samples), the numbers of gynoparae and males found on 300 randomly chosen leaves per tree were recorded each week. The survey ended with leaf fall, which is the ultimate date for the oviparae (sexual females) to mature and lay frost-resistant eggs.

Genetic analyses

Genetic analyses were performed on a sample of individuals collected on each date of the population dynamics survey. The genetic study was restricted to two sites.

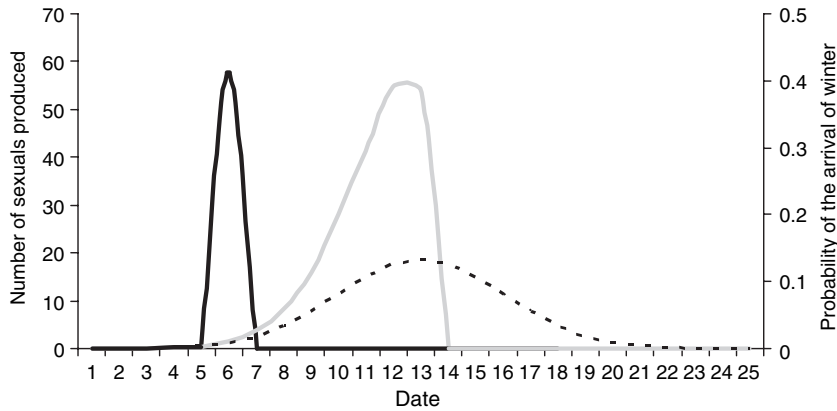


Fig. 2 Dynamics of production of sexual forms predicted by the model at ESS. Black line: ESS corresponding to constraining the time window for the production of sexual forms to a single date (sexual strategy). Grey line: ESS with no constraint on the length of time for the production of sexual forms (facultative asexual strategy). Dashed line: probability distribution of the ultimate date of suitability of the winter host (great winter unpredictability). Parameter values of the model: $\lambda = 1.3$; $\sigma = 3$.

The size of each sample (defined by week + tree) was about 30 gynoparae and 15 males. A total of 420 gynoparae and 169 males were typed at seven microsatellite loci. For gynoparae, all 12 samples (from mid-September to late November) originating from one site were analysed. In addition, three weekly samples (weeks 3, 5 and 8) collected at the second site were analysed to test for between-sites differentiation. For males, all samples originating from both sites were analysed. DNA extraction, PCR amplification and allele scoring were performed according to Halkett *et al.* (2005a). Samples of gynoparae and of males collected in the same week on different trees showed no significant genetic differentiation, even between sites (Fisher exact tests, $P > 0.237$). Thus individuals from the two sites were pooled by week in the subsequent analysis (subsequently denoted 'week samples'). Gynoparae and males were assigned (according to their ancestry coefficient q_i) to sexual or facultative asexual reproductive mode using Bayesian clustering (Pritchard *et al.*, 2000), following Halkett *et al.* (2005a). Briefly, runs were set to a burning-in period of 60 000 iterations followed by 600 000 iterations, assuming an uninformative priors for q_i . The threshold for assignment was set at $q_i > 0.9$. The two clusters had distinct genetic characteristics (e.g. Hardy-Weinberg and linkage disequilibria absent in the sexual cluster but strongly significant in the facultative asexual one, Balloux *et al.*, 2003; Halkett *et al.*, 2005b), and joint assignment of several reference lineages of known reproductive mode (previously studied in the laboratory) enabled the two genetic entities to be confidently labelled (Halkett *et al.*, 2005a). The dynamics of colonization of the two reproductive modes was then estimated from the proportion of individuals in each sample belonging to sexual or facultative asexual clusters.

Results

Prediction of the improved model

New simulations predicted that constraining the time interval of production of sexual forms would result in

selection of a sexual strategy characterized by an early switch to sexual reproduction, occurring at the very beginning of the arrival of winter (Fig. 2, black line). Conversely, an unconstrained facultative asexual strategy would tend to delay the investment in sexual reproduction and to spread it until the most probable date for the arrival of winter (Fig. 2, grey line).

Observed temporal population dynamics and genetics

Colonization of mating sites by gynoparae occurred over the whole sampling period (Fig. 3a, dashed line). A plateau was reached at week 2, lasting until week 6. Then a second increase in the abundance of gynoparae was observed, suggesting bimodality in colonization

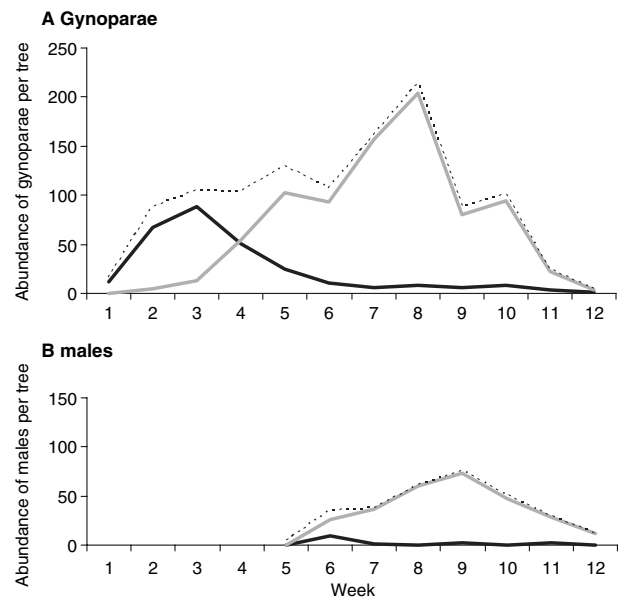


Fig. 3 Observed dynamics of colonization of mating sites by gynoparae (a) and males (b). Dashed curve: total abundance. Black: abundance of sexual lineages; grey: abundance of facultative asexual lineages.

dynamics. Males followed roughly the same pattern, but were much fewer and began to arrive on mating sites 3–4 weeks after the first gynoparae, as usually reported for *R. padi* (Dixon, 1971; Austin *et al.*, 1996).

About 98% of the gynoparae analysed genetically were assigned unambiguously to a reproductive mode: 70% belonged to the facultative asexual cluster and 28% to the sexual one. Gynoparae produced by sexual lineages formed the major part of the samples during the first 3-week samples, although gynoparae from facultative asexual lineages was not detected until the third sample and became dominant after the fifth (Fig. 3a). Similarly, 98% of sampled males were unambiguously assigned to a reproductive mode. In total, more than 94% of the males belonged to the facultative asexual cluster. This extreme proportion of facultative asexual individuals in the male samples could result from the high frequency of facultative asexual lineages that produce only males (Simon *et al.*, 1991; Halkett *et al.*, 2005a). Nonetheless, as for gynoparae, most of the rare males that belonged to the sexual cluster arrived early at mating sites (Fig. 3b).

Discussion

In this study, both theoretical predictions and empirical data suggest that sexual lineages invest earlier in the production of sexual forms than do facultative asexual lineages. This results in temporal structuring of mating site colonization, such that sexual and facultative asexual lineages coexist in space but not in time. *In natura*, this pattern was particularly obvious in gynoparae: individuals originating from sexual lineages were strongly dominant during the first 3 weeks of colonization. Individuals produced by facultative asexual lineages largely predominated thereafter. Facultative asexual lineages were sampled over a longer period than were sexual lineages, consistent with the assumptions of the model. Nonetheless, the arrival of gynoparae originating from sexual lineages is slightly more spread than expected, which might simply denote a lack of synchrony among these lineages. The temporal pattern observed here makes sense, because an unusually early arrival of winter combined with a harsh winter may eliminate sexual lineages that did not produce eggs before the arrival of winter, whereas it is not fatal for the facultative asexual lineages as they spread the risk and produce both sexual and asexual forms over a prolonged time. It is noteworthy that the predominance of the facultative asexual lineages is in agreement with the great climatic unpredictability of the location under scrutiny (western France). The ratio between sexual and facultative asexual lineages is expected to differ among locations: for example, continental areas (such as Eastern Europe) characterized by harsh winters (Halkett *et al.*, 2004) should favour the sexual strategy, which is consistent with observations (Papura *et al.*, 2003).

Sexual and facultative asexual lineages often differ in their allocations of resources to various traits (e.g. growth, dispersal and resting forms) as a direct consequence of the level of investment in sexual reproduction (Smith, 1978; Eckert, 2002; Simon *et al.*, 2002; De Meester *et al.*, 2004). In aphids, careful examination of fitness components has revealed no difference between sexual and facultative asexual lineages during the common parthenogenetic phase of their life cycles (Rispe *et al.*, 1996; Vorburger *et al.*, 2003b; Vorburger, 2004). In contrast, sexual lineages of cyclical parthenogenetic organisms (including aphids) are thought to benefit from sexual reproduction through the exclusive production of eggs resistant to adverse climatic conditions (De Meester *et al.*, 2004). We now add that sexual and facultative asexual overwintering strategies should also differ in the time of investment in sexual reproduction.

Differences in flowering periods of sexual and facultative asexual plants are known in some apomictic species (Verduijn *et al.*, 2004), but have never been correlated with specific ecological and evolutionary strategies. As in diapausing insects, facultative asexual plants could be considered as performing a 'bet-hedging' strategy allowing them to deal more efficiently with environmental uncertainty (Menu *et al.*, 2000; Halkett *et al.*, 2004). To take the analogy further, it would be of interest to identify the main predictive factors for sexual reproduction in plants (adverse climatic conditions, parasitism, pollination, etc.) and to assess precisely the dynamics of flowering of both types.

Although our modelling approach does not strictly account for the coexistence of the two strategies – as they arose from independent simulations – the consistent findings of an earlier arrival of sexual lineages at mating sites provided by the observations and the model predictions suggested that coexistence could result simply from a temporal separation of two populations functioning almost as distinct entities. Ecological specialization of sexual and facultative asexual lineages often relies on heritable traits, which can lead to local population adaptation (Ceplitis, 2001; Dedryver *et al.*, 2001). Irrespective of the origin of asexual lineages (Delmotte *et al.*, 2001), the (partial) removal of sexual reproduction drastically reduces gene flow between sexuals and asexuals (Delmotte *et al.*, 2002), thus favouring the establishment of a differential selective regime (disruptive selection). Further reduction of gene flow could lead to complete separation of genetic entities and ecological speciation (Via, 2001; Lenormand, 2002), as shown in many phytophagous insects (Via, 2001; Drès & Mallet, 2002).

This brake on gene flow is often associated with spatial isolation of populations, as observed in cases of geographical parthenogenesis (Pongratz *et al.*, 2003; Van Dijk, 2003; Vorburger *et al.*, 2003a), and speciation is then regarded as allopatric (Kirkpatrick & Ravigné, 2002). The present work emphasizes the importance of the temporal dimension of the ecological niches that could result in

fine-scale temporal population genetic structure, in which sexual and facultative asexual lineages experienced reduced interactions that could even lead to allochronic speciation (Abbot & Withgott, 2004).

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