

Timing of dispersal: effect of ants on aphids

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Abstract Mutualists can affect many life history traits of their partners, but it is unclear how this translates into population dynamics of the latter. Ant–aphid associations are ideal for studying this question, as ants affect aphids, both positively (e.g., protection against natural enemies) and negatively (e.g., reduction of potential growth rates). The unresolved question is whether these effects, which have been observed at the level of individuals and under controlled environmental conditions, have consequences at the population level. On estimating aerial aphid populations by using weekly suction trap data spanning up to

22 years from different locations in France, we show that in ant-attended aphid species long-distance dispersal occurs significantly later, but that the year-to-year changes in the peak number of migrants are not significantly lower than for non-attended aphids. Host alternation had the same retarding effect on dispersal as ant attendance. We discuss the delay in the timing of dispersal in ant-attended aphids, and potential costs that arise in mutualistic systems.

Keywords Ant attendance · Dispersal · Mutualistic systems · Suction traps

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Introduction

Timing of dispersal in insects is a crucial determinant of their fitness. For example, delay in arriving at the host plant, thus missing the period when the plant is of the best nutritional quality, can reduce the growth rates of herbivorous insects (Mattson 1980; White 1993). Similarly, natural enemies are likely to focus on aggregated and most abundant prey (Ives et al. 1993)—and the best response of prey is proper timing of emigration from large aggregations (Muller-Landau et al. 2003). It is unknown, however, whether mutualists can also affect timing of dispersal and population fluctuations of their partners.

The ant–aphid interactions are well-suited for studying these questions. In controlled laboratory experiments, ant-attended aphid colonies produced lower proportions of winged morphs and attained higher local population sizes than unattended colonies (El-Ziady and Kennedy 1956; Way 1963). The likely reason is that ants protect aphids against natural enemies, and therefore aphids are

less induced to escape from their natural enemies by dispersal (Dixon and Agrawala 1999; Müller and Godfray 1999; Kunert and Weisser 2003). Ant attendance also significantly reduced population growth rates in facultatively ant-attended aphid species (Stadler and Dixon 1998; Yao et al. 2000; Stadler et al. 2002). The explanation is that the metabolism associated with the production of more and high-quality honeydew is incurring costs when aphids need to adjust the sugar and amino acid composition in response to the presence/absence of ants (Fischer and Shingleton 2001; Yao and Akimoto 2001).

These laboratory results suggest two hypotheses that can be tested in the field: (a) being protected against natural enemies, ant-attended aphid species should disperse later than unattended species, and (b) given that ants slow down the population growth rate of facultative myrmecophiles and temporarily shelter their partners from natural enemies, smaller year-to-year changes in the numbers of ant-attended species should be expected. No attempt has yet been made to study these hypotheses, possibly because population data on dispersing morphs are difficult to obtain. Here we present an example of the impact of ants on long-distance dispersal of 33 aphid species in the field, using suction trap data from different locations in France, which were collected during a maximum of 22 years. We do so by controlling for host alternation and by including potential confounding aspects like geographical location and associated differences in climatic conditions (Dixon et al. 1993) in our analysis.

Methods

Data on aphid flight dynamics were obtained from suction traps (Macaulay et al. 1988) catching flying aphids at about 12 m above ground by means of constant 45 m³/min airflow. The catches belong to the AGRAPHID network sites in France (Hullé 1995) and range from 10 to 22 years of collection (Table 1). For each site (see Fig. 1 for their location), the data consist of weekly counts of migrants. In total, 33 aphid species were determined in the catches (Table 2). Their degree of ant-attendance was determined after Börner (1952), Müller (1984), Blackman and Eastop (1994, 2000), and Kloft and Kunkel (1985).

Aphids produce winged morphs over a period of several weeks. The proportions of these that are caught in suction traps vary, however, considerably, as the catches are highly random. Thus, for the estimate of the week of peak dispersal in each season, $w_{\max}(s,t)$, we did not use the week when the maximum number of migrants was caught in the suction traps, but estimated it at each site as the weighted average for the whole series of catches:

Table 1 Locations of the suction traps in France. Years when aphids were sampled at individual sites are indicated by x symbol

| Site | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | |
|-------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|---|
| Arras | x | | | | | | | | | | | | | | | | | | | | | | |
| LeRheu | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x |
| Colmar | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x |
| Orleans | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x |
| Montpellier | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x |
| Versailles | | | | | | | | | | | | | | | | | | | | | | | |
| Loos | | | | | | | | | | | | | | | | | | | | | | | |

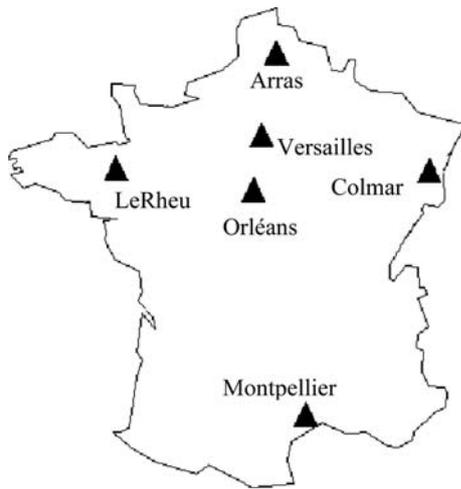


Fig. 1 Location of the suction traps within France, from where our data originate

$$w_{\max}(a, s, t) = \frac{\sum_{i=1}^{35} i \cdot c(a, s, t, i)}{\sum_{i=1}^{35} c(a, s, t, i)},$$

where *a* is aphid species, *s* is site, *t* is year, *i* is the number of week in the year, *c*(*a*, *s*, *t*, *i*) the number of individuals of species *a* caught in suction trap at site *s* in year *t* and week *i*. The average was calculated only for the first 35 weeks in the year, in order to exclude the second peak in abundance of migrants that sometimes occurs in aphids in the autumn (Dixon 1998), which is preceded by a period of aestivation approximately during weeks no. 35 ± 2. The average week of peak dispersal of ant-attended species during the observation period at site *s* was then calculated as

$$w_A(s) = \frac{\sum_{t=1, a \in A}^{t_s} w_{\max}(a, s, t)}{t_s}$$

and that of non-attended species as

$$w_{NA}(s) = \frac{\sum_{t=1, a \notin A}^{t_s} w_{\max}(a, s, t)}{t_s},$$

where *A* is the set of ant-attended species and *t_s* the number of years for which data were available at site *s*. This procedure provides an estimate of the between-year variability in the aerial populations.

For the sites with the longest (>18 years) data series and for each species, the coefficient of variation of the maximum numbers of migrants caught during the year over all years of observation, *CV*(*a*,*s*), was calculated as

$$CV(a, s) = \frac{STDEV(\max_i(c(a, s, t, i)))}{\text{average}(\max_i(c(a, s, t, i)))} \times 100.$$

Then the averages of *CV*(*a*,*s*) for all ant-attended species, *CV_A*, and for all non-attended species, *CV_{NA}*, were calculated.

Statistical significance of the differences between the peak weeks of dispersal was analysed by means of a three-way ANOVA with interactions with factors ants, site, and year. Statistical significance of the differences between the coefficients of variation of the maximum numbers of migrants was analysed by means of a two-way ANOVA with factors ants and site. Possible confounding effect of host alternation on the timing of peak dispersal was analysed by means of a two-way ANOVA with repeated measurements and factors ant attendance and host alternation. For all ANOVAs, only the largest subset of available data was used, for which data from all years at all sites were available: data from LeRheu, Colmar, Orleans and Montpellier from the years 1978–1996 (see Table 1), i.e., 19 years of data from four sites.

Results

In total, 21 unattended and 12 myrmecophilous aphid species were identified in the suction trap catches. Figure 2a shows the average week of peak dispersal during the observation period at each site, as indicated by suction-trap catches, separated for unattended and ant-attended aphid species at the seven sites. Except for the catches at Montpellier, the peak in dispersal of ant-attended species was 0.5–2.5 weeks later compared to the unattended species. Table 3 shows the results of a three-way ANOVA with interactions of the factors ants, site, and year. All three factors had a statistically highly significant (*P* < 0.01) influence on the timing of dispersal of the species studied. Interactions, except for ants × site and site × year, were not significant.

Figure 2b shows the average coefficient of variation in peak numbers for all ant-attended species, *CV_A*, and that for all non-attended species, *CV_{NA}*. In three out of four sites the attended aphid species showed a lower variability in the size of peak catches than unattended aphid species. Table 4 shows the results of a two-way ANOVA with factors ants and site. Site had a statistically significant (*P* < 0.05) influence on the average coefficient of variation, but ants did not. Two-way repeated measures ANOVA revealed a significant effect of both ant attendance and host alternation on the timing of peak dispersal (Table 5), while interaction effects were not significant. On average, peak dispersal in host alternating aphids was 0.9 week later than for non-host alternating aphids.

Table 2 List of aphid species indentified in the suction traps, their degree of myrmecophily according to Börner (1952), Müller (1984), Kunkel and Kloft (1984), Blackman and Eastop (1994, 2000), personal observations and personal communication and presence/absence of host alternation

| Species | Host alternation | Myrmecophily |
|---|------------------|--------------------------|
| <i>Acyrtosiphon pisum</i> | Paramonoecious | Not attended |
| <i>Aphis craccivora</i> | Monoecious | Facultative myrmecophile |
| <i>Aphis fabae</i> | Dioecious | Facultative myrmecophile |
| <i>Aploneura lentisci</i> | Dioecious | Not attended |
| <i>Appendiseta robiniae</i> | Monoecious | Not attended |
| <i>Brachycaudus helichrysi</i> | Dioecious | Facultative myrmecophile |
| <i>Brachycaudus (Thuleaphis) amygdalinus</i> | Dioecious | Facultative myrmecophile |
| <i>Brachycaudus (Thuleaphis) rumexicolens</i> | Dioecious | Facultative myrmecophile |
| <i>Brevicoryne brassicae</i> | Paramonoecious | Not attended |
| <i>Capitophorus elaeagni</i> | Dioecious | Facultative myrmecophile |
| <i>Capitophorus hippophaes</i> | Dioecious | Facultative myrmecophile |
| <i>Cavariella aegopodii</i> | Dioecious | Not attended |
| <i>Dysaphis (Pomaphis) plantaginea</i> | Dioecious | Facultative myrmecophile |
| <i>Elatobium abietinum</i> | Monoecious | Not attended |
| <i>Hoplocallis pictus</i> | Monoecious | Not attended |
| <i>Hyperomyzus lactucae</i> | Dioecious | Not attended |
| <i>Macrosiphum euphorbiae</i> | Dioecious | Not attended |
| <i>Metopolophium dirhodum</i> | Dioecious | Not attended |
| <i>Metopolophium festucae</i> | Monoecious | Not attended |
| <i>Microlophium carnosum</i> | Monoecious | Not attended |
| <i>Myzocallis (Agrioaphis) castanicola</i> | Monoecious | Not attended |
| <i>Myzus cerasi</i> | Dioecious | Facultative myrmecophile |
| <i>Phorodon humuli</i> | Dioecious | Not attended |
| <i>Pterocallis alni</i> | Monoecious | Not attended |
| <i>Rhopalosiphum insertum</i> | Dioecious | Facultative myrmecophile |
| <i>Rhopalosiphum padi</i> | Dioecious | Facultative myrmecophile |
| <i>Schizaphis graminum</i> | Paramonoecious | Not attended |
| <i>Sitobion avenae</i> | Paramonoecious | Not attended |
| <i>Sitobion fragariae</i> | Monoecious | Not attended |
| <i>Thelaxes dryophila</i> | Monoecious | Facultative myrmecophile |
| <i>Therioaphis trifolii</i> | Paramonoecious | Not attended |
| <i>Tuberculatus (Tuberculoides) annulatus</i> | Monoecious | Not attended |
| <i>Tuberculatus (Tuberculoides) eggleri</i> | Monoecious | Not attended |

Monoecious Aphids feed on a single host plant throughout the year. *Dioecious* Aphids feed on a winter host (trees, bushes) and summer hosts (herbs, grasses). *Paramonoecious* Aphids migrate between winter and summer hosts, but the winter host is a non-woody plant

Discussion

It is now well established that ants can have both positive and negative effects on the partners they attend. Costs for aphids comprise changes in honeydew metabolism (Yao and Akimoto 2001; Fischer and Shingleton 2001), predation by ants (Sakata 1994), competition for mutualists (Addicott 1978) or fitness costs (Stadler et al. 2002; Stadler 2004), to name a few. Benefits are associated with the protective function of ants (Nixon 1951; Tilles and Wood 1982), hygienic services (Buckley 1987) or higher growth rates, e.g., in obligate myrmecophiles (Flatt and Weisser 2000). The evolutionary significance of ant-induced changes in timing of dispersal and variability in population size of ant-attended aphids is less clear.

Host plant quality is usually high for aphids in spring and sometimes in autumn, when the plants produce new leaves or shoots and when nutrients are exported from the leaves (Kennedy et al. 1950; Dixon 1970). Aphids need to find hosts of the highest quality to maximise reproduction. In a recent study, host quality was found to be significantly more important for potential growth rates of facultative myrmecophiles than ant attendance (Stadler et al. 2002), indicating a strong selection pressure operating on aphids to optimise the timing of dispersal for finding high quality host plants. Retardation in dispersal thus may have a twofold impact on aphid population dynamics. It might be advantageous for aphids to build up large numbers producing a flush of migrants, but it also may incur costs, as the host plants which the migrants eventually arrive at may

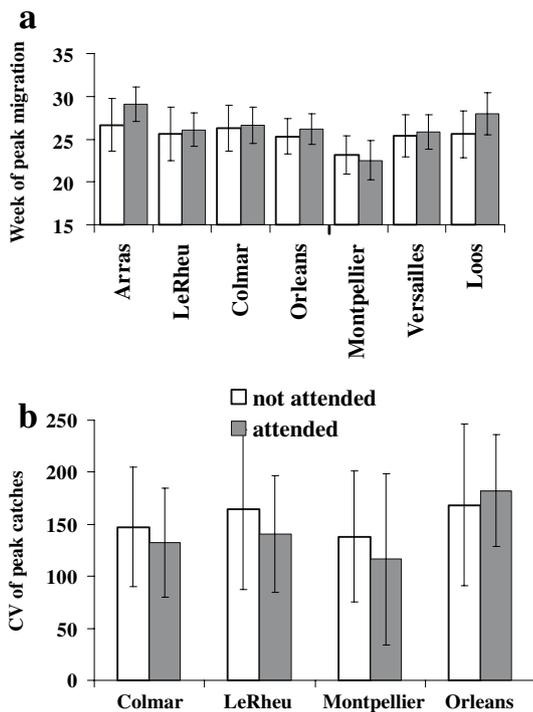


Fig. 2 Timing of peak migration (a) and coefficients of variation (CV) of peak catches (b) of winged aphids in different suction trap locations separated for ant-attended and for unattended species. Vertical bars indicate 1 SD

be in a more advanced state of development and of poor quality. Thus, the potential additional cost of ant attendance, unappreciated so far, could be a reduced probability of finding high quality hosts during summer and a lower rate of increase after dispersal compared to those individuals, which dispersed earlier. The delay in dispersal of attended species ranges between 0.5 and 2.5 weeks

(Fig. 2a), and is equivalent to about one complete aphid generation, which could be produced on the new host. This potential mismatch in the timing of dispersal and associated reduction in fitness corroborates recent findings that mutualistic associations with ants carry significant indirect costs, and accounts for the rarity of honeydew and nectar producers that show close associations with ants (Bristow 1991; Stadler et al. 2001). The tendency to lower inter-annual variation in population fluctuations (Fig. 2b) of ant-attended aphids, albeit not significant, might be a direct consequence of their reduced growth rates and partial protection from natural enemies making population fluctuations less erratic. This trend was shown in three out of four sites.

Some aphids are associated with ants, while closely related species (even within the same genus) are not, even if they feed on the same plant organ. This fact probably indicates that in different environments both strategies have advantages as well as disadvantages. Thus, relative to unattended aphids any deviation from the optimal dispersal function (and time of peak dispersal is a valid proxy for this distribution) carries costs for attended aphids, and thus should be under selection.

The significant interactions between the factors ants and site and between site and year (Table 3) appear to be a consequence of the north–south or seaside-continental gradients in the locations of the suction traps. It is likely that ant abundance or temperature-dependent processes change along these gradients. For example, Hanski and Woiwood (1993) concluded from suction-trap data of the Rothamsted Insect Survey that large-scale spatial patterns in the dynamics of aphid populations are largely driven by regional stochasticity (variable weather conditions). However, the presence of these interactions does not affect the

Table 3 Results of the three-way ANOVA with factors ants, site and year, and peak of aphid dispersal as dependent variable. Data originate from suction traps at four sites, comprising 19 years of continuous sampling

| Factor | df effect | MS effect | df error | MS error | F | P level |
|--------------------|-----------|-----------|----------|----------|--------|---------|
| Ants | 1 | 200 | 1,884 | 8.71 | 22.98 | <0.01 |
| Site | 3 | 964 | 1,884 | 8.71 | 110.56 | <0.01 |
| Year | 18 | 185 | 1,884 | 8.71 | 21.22 | <0.01 |
| Ants × site | 3 | 57 | 1,884 | 8.71 | 6.55 | <0.01 |
| Ants × year | 18 | 8 | 1,884 | 8.71 | 0.91 | 0.57 |
| Site × year | 54 | 16 | 1,884 | 8.71 | 1.85 | <0.01 |
| Ants × site × year | 54 | 5 | 1,884 | 8.71 | 0.54 | 1.00 |

Table 4 Results of the two-way ANOVA with factors ants and site and coefficients of variation as dependent variable

| Factor | df effect | MS effect | df error | MS error | F | P level |
|--------|-----------|-----------|----------|----------|------|---------|
| Ants | 1 | 3,853 | 117 | 4,476 | 0.86 | 0.36 |
| Site | 3 | 12,450 | 117 | 4,476 | 2.78 | 0.04 |
| Error | 3 | 2,287 | 117 | 4,476 | 0.51 | 0.68 |

Table 5 Results of the two-way repeated measures ANOVA with factors ants and host alternation and peak of aphid migration as dependent variable

| | df effect | MS effect | df error | MS error | F | P level |
|------------------------|-----------|-----------|----------|----------|-------|---------|
| Ants | 1 | 452 | 1,998 | 11.76 | 38.41 | <0.01 |
| Host alternation | 1 | 258 | 1,998 | 11.76 | 21.97 | <0.01 |
| Ant × host alternation | 1 | 29 | 1,998 | 11.76 | 2.50 | 0.11 |

general conclusion, and the results are robust along these gradients. Although we focused our analysis only on the effects of ants on aphids, we believe that similar results could be obtained for other groups of insects comprising ant-attended and unattended species, such as coccids or membracids. However, it is likely that the effect of ants on the timing of dispersal and potential costs of a delayed dispersal is most pronounced in fast-reproducing organisms, such as aphids, because of the relative importance of feeding on high-quality hosts.

Peak dispersal occurred significantly later in host-alternating species. Nevertheless, the corresponding ANOVA (Table 5) revealed a simultaneous highly significant effect of ant attendance, while interactions were not significant. This means that in addition to differences in climatic conditions (also included in the factor site, Table 3) there are two factors, host alternation and ant attendance, acting independently in the same direction: delaying the peak of dispersal.

In summary, our results support the first hypothesis, but the available suction-trap data currently do not support the second: in ant-attended species dispersal is delayed, but the year-to-year population fluctuations were not proven to be less variable compared with unattended aphid species. Nevertheless, this suggests that mutualistic associations between aphids and ants affect large-scale population features such as long-distance dispersal and that the potential consequences associated with a delayed dispersal should also be accounted for when studying the cost and benefits in mutualistic associations.

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