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Should I stay or should I go?

The role of dispersal and cannibalism in exploitation strategies of a predatory mite

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Timing of aerial dispersal is a heritable trait in the predatory mite *Phytoseiulus persimilis*

A.M. Revynthi, D. Verkleij, A. Janssen & M. Egas

ABSTRACT — Dispersal is a main determinant of the dynamics and persistence of predator-prey metapopulations. Theoretical studies predict the existence of two types of dispersal strategies: the Milker, an early dispersal strategy, and the Killer, a late dispersal strategy. In the predatory mite *Phytoseiulus persimilis*, empirical studies have suggested a genetic component for timing of aerial dispersal in the presence of prey. We tested this by selecting for early and late dispersers from rose leaves with two-spotted spider mites as prey, showing that 6 rounds of selection for early or late dispersal resulted in predator lines displaying earlier or later dispersal. In a population dynamics experiment, we furthermore show that selection for timing of dispersal also results in predicted differences in the local interaction time with the prey and in the cumulative number of dispersers. We conclude that timing of dispersal is a heritable trait that can be selected for and results in lines with quantitative differences in local predator-prey dynamics. This opens ways to experimentally investigate the evolution of alternative prey exploitation strategies.

INTRODUCTION

Dispersal is a key process in the persistence of predator-prey metapopulations and has major consequences for individual fitness and for population dynamics (Janssen et al. 1997; Zemek and Nachman 1998, 1999; Ellner et al. 2001; Revilla et al. 2004; Bowler and Benton 2005, 2009; Clobert et al. 2009). Even when local predator-prey populations go extinct, persistence is observed at a metapopulation level because of the asynchronies of the dynamics in these local populations and the founding of new populations by dispersing individuals (Vandermeer 1973; Hilborn 1975; Crowley 1981; Jansen and Sabelis 1992; Janssen et al. 1997). The adaptive value of dispersal is determined by the balance between its costs and benefits, which are highly dependent on the life stage and condition of an individual, as well as on the local and environmental conditions (Bowler and Benton 2005, 2009; Bonte and Dahirel 2016).

From the perspective that dispersal is a life-history trait (Bonte and Dahirel 2016) and that the decision to disperse from a patch is not only context-dependent but also heritable, we can consider predator dispersal as a prey exploitation strategy (van Baalen and Sabelis 1995; Sabelis et al. 2002). Generally, the argument runs as follows: In a local predator-prey population with a limited interaction period, early predator dispersal decreases predation, resulting in a longer interaction period between the predators and their prey. As a consequence, the predator offspring will have more food available, and this prudent predation will therefore result in the production of more dispersing offspring during the total interaction period. However, a longer interaction period can lead to higher risk of secondary predator invasions. These invaders may not disperse early and exploit the prey population to their own interest by consuming the prey that prudent predators saved for their offspring (van Baalen and Sabelis 1995). Hence, a local population of prudent predators can be invaded by selfish predators that will benefit from them, so prudent predation is not evolutionary stable in well-connected metapopulations because prudent predators are outcompeted by cheaters (cf. Maynard Smith 1964). In an earlier theoretical paper, van Baalen and Sabelis (1995) named the selfish strategy Killer and the prudent Milker. Theory predicts that Milker-like strategies will be favored only when local predator populations are sufficiently isolated from each other, thus reducing the risk of invasions of Killers (van Baalen and Sabelis 1995; Pels and Sabelis 1999; Pels et al. 2002).

Empirical evidence supporting these theoretical predictions is scarce and incomplete. Pels and Sabelis (1999) investigated the dispersal strategies of several field populations of the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae), and found that an isofemale line of predators from a coastline population, where subpopulations are well-connected by dispersal, only dispersed when prey patches were depleted. In contrast, another isofemale line of predators from an inland population, where subpopulations are isolated from each other, dispersed before the prey patch was entirely depleted. In addition, dispersal before prey depletion was associated with a longer interaction period and, in some cases, increases of prey numbers during this period (Pels and Sabelis 1999). In addition, Revynthi et al. (CHAPTER 2) collected predatory mites of the same species from six sites along the coast of Turkey and from five sites in Sicily, and investigated their dispersal behavior and population dynamics in a set-up similar to that of Pels and Sabelis (1999). The

collected strains showed large variation in prey exploitation strategies and significant differences in dispersal rate.

Together, these studies show that there is variation among lines and populations in behavior regarding prey exploitation and timing of aerial dispersal, and suggest that there is a genetic component for dispersal tendency. However, evidence of genetically determined alternative dispersal strategies remains absent. Taking into account that previous research regarding alternative dispersal strategies assumed that aerial dispersal rates have a genetic component (Pels and Sabelis 1999; Revynthi et al., CHAPTER 2), we investigated whether it is possible to select for Milker-like and Killer-like predatory mite lines in a bidirectional artificial selection experiment, i.e., one line selected for early aerial dispersal, the other for late dispersal. The timing of dispersal in these selection lines was compared to control (unselected) lines. Furthermore, we confirmed these differences in dispersal behavior in a population dynamics experiment, which also served to test the theoretical predictions that such differences should result in differences in the interaction period and the total number of dispersers from these patches.

MATERIALS AND METHODS

Roses

Young rose plants (Olij Rozen, De Kwakel, the Netherlands) were transferred to a climate room, where they were hydroponically grown on rock wool. Conditions in the climate room were 25 °C, 70% RH and 16L:8D. The rose plants were watered 2× per week and fertilized (20-10-20 N-P-K) once per week.

Spider mites

Two-spotted spider mites (*Tetranychus urticae* Koch) were originally collected from cucumber plants in a commercial greenhouse in May 1994 (Pallini et al. 1997). The spider mite culture was kept on Lima bean plants (*Phaseolus lunatus* L.) in a climate room at 26 °C, 50% HR and 16L:8D.

Cohorts were created to obtain adult females of approximately 2 days into adulthood. One hundred and fifty adult female spider mites were divided over the two primary leaves of a Lima bean plant. The leaves were placed on a bed of water-saturated cotton wool in a plastic tray, which kept them turgid, and prevented the spider mites from dispersing because spider mites cannot walk over wet cotton wool. The females were left on the bean leaves to oviposit for 48 h, after which they were removed and their offspring were allowed to develop. The cohorts were kept in a climate room at 25 °C, 65% RH and 16L:8D, for 17 days.

Predatory mites

To ensure sufficient genetic variation for selection to act on, a base population was created by mixing predatory mites from six strains collected in Turkey in 2013 and five strains from Sicily in 2014, which were shown to harbor significant variation in dispersal rate (Revynthi et al., CHAPTER 2). Two gravid females of each of the 11 strains were haphazardly selected and placed on Lima bean leaflets (*P. lunatus*) infested with two-spotted spider mites (*T. urticae*). Cultures of predatory mites were kept as described in Pels and Sabelis (1999). In short, the bean leaflets were isolated on a plastic float, which was placed in a plastic tray,

which was filled with a 15-mm layer of water with dissolved soap. In order to reduce selection for mites with higher dispersal tendency the plastic float was covered with a plastic aquarium (19.5 × 13.0 × 11.5 cm) with a piece of fine-meshed flexible gauze (80 µm) hanging from the ceiling that connected to the float/leaflets. In this way the mites had the opportunity to leave the leaves with prey and consequently return without drowning. This method ensured that the predators that left the prey patch did not disappear; hence, it reduced the selection for predators that did not disperse in the presence of prey (i.e., Killers).

Rectangular holes were made in the ceiling of the aquaria and were covered with fine mesh (80 µm) for ventilation. Individual plastic trays were placed in a fine mesh (80 µm) cage. The cultures were fed 3× per week by adding two spider mite-infested Lima bean leaflets to the floats and were kept in a climate room at 25 °C, 70% RH and 16L:8D.

To obtain sufficient numbers of gravid females of the same age (2 days old) for selection and experiments, cohorts were created as follows. Ten gravid female predatory mites from the base population were placed on a spider mite-infested bean leaf on a bed of water-saturated cotton wool in a Petri dish (14 cm diameter, 2 cm height). In this way, the leaves remained turgid for at least 10 days. The gravid females were allowed to oviposit for 48 h, after which they were removed and only their eggs and prey were left on the leaves. The cohorts were kept in a climate room at 25 °C, 70% RH and 16L:8D, for 10 days.

Selection procedure

For the experimental set-up of the selection procedure, 9 wind tunnels were prepared as in Revynthi et al. (CHAPTER 2) for each round of selection. Each wind tunnel consisted of a plastic aquarium (25.3 × 15.8 × 15.5 cm) with holes (11.5 cm diameter) on both sides, covered with a fine mesh (80 µm). A fan was placed in front of the mesh on one side and created a constant air flow inside the wind tunnel, which was kept at approximately 0.4 m/s during the selection. The shoots of two rose leaves, each with five leaflets, were inserted in a plastic vial (24.5 mm diameter, 40 mm height) filled with water-saturated Oasis floral foam and the vial was placed at the upwind end of the wind tunnel. The width and length of the leaves ranged from 5-7 cm and 8-10 cm, respectively. Each of the rose leaves was infested with 10 adult female spider mites, 24 h prior to the selection procedure. At the downwind side of the wind tunnel, a trap was placed in order to capture the aerially dispersing predatory mites. The trap consisted of a Petri dish containing the three top leaflets of a rose leaf with spider mites, with the shoot (ca. 3 cm) inserted through a hole in the lid of an Eppendorf tube (1.5 ml) filled with wet Oasis floral foam.

Early dispersal line

In the first round of selection for early dispersal, 60 gravid predator females were transferred from the cohorts to upwind rose leaves in each of six wind tunnels. At 2, 4, 6, 8 and 24 h, the trap leaves were replaced with new ones, the dispersed mites on the trap leaves were counted and the first 20-25 dispersers of each of the six wind tunnels were used to set up a culture of the early-dispersal line. The remaining 210-240 individuals were discarded. Simultaneously, another 60 gravid predator females were transferred to upwind rose leaves in three other wind tunnels. Using the same time intervals, all dispersed predatory mites were collected, transferred into a common cage and 120 of them were randomly chosen at

the end of the 24 h and used to start a control line. Both lines were kept in rearing units as described above. Subsequently, cohorts were created using gravid females from the selection line and control line 7 days after the selection, and the adults from these cohorts were subjected to a new round of selection. The total procedure was repeated for six rounds.

Late dispersal line

Instead of selecting for predators that did not disperse and running the risk that this would include sick or otherwise disabled mites, we selected for late dispersers in a similar manner as above, except that the 20-25 predators that had dispersed last (within 24 h) were used to set up this line. A separate control line was started simultaneously in three separate wind tunnels as above. This selection procedure was also repeated for six rounds.

For logistic reasons, selection of the two lines could not be run simultaneously. Moreover, a period of 14 days between selection rounds of each line was required to obtain a new generation of adult offspring. Therefore, selection of the early-dispersal line and its control were alternated with the late-dispersal line and its control.

Selection response experiment

After six rounds of selection, the dispersal rates of the selected lines and control lines were measured in a set-up similar to that of the selection procedure. To standardize the quality of the prey patch from which the predators dispersed, these only contained spider mite web, prey eggs and no other prey stages. Furthermore, the patch consisted of one rose leaf only, but was otherwise similar to those in the selection procedure. Prior to the experiment, 15 2-day-old adult female spider mites were allowed to oviposit for 48 h on this leaf, and then were removed and the number of spider mite eggs was reduced to 80 per leaf, which was subsequently used for the experiment. A trap was placed at the downwind side of the wind tunnel, as described above (*Selection procedure*).

At the start of the experiment, 30 gravid 2-day-old female predators from the selection line or its respective control line were placed on the prey patch. The mites that had dispersed to the traps were counted during 8 h with 2-h intervals. At the end, the predators remaining on the prey patch were counted. The response experiment was performed in three blocks of four replicates of each selection line and its respective control line. The response to early-dispersal selection and late-dispersal selection were measured in separate blocks.

Population dynamics experiment

To measure dispersal of the selected lines in a population dynamics context, eight wind tunnels were prepared as in Revynthi et al. (CHAPTER 2) (see also *Selection procedure*). The experimental procedure followed was the same as in Revynthi et al. (CHAPTER 2): eight rose leaves were infested with 15 2-day-old adult female spider mites, each placed in a wind tunnel and one gravid 2-day-old adult female predatory mite was released on each leaf 48 h later. From this day on, adult prey and predators on the leaf and dispersers in the wind tunnel were counted every 24 h until there were no more mites (either prey or predators) present on the leaf. This experiment was performed in two blocks of four replicates for each selection line.

Statistical analysis

We tested for differences in time to dispersal between the various lines with a time-to-event analysis with a Cox proportional hazard model. Censoring was applied to predators that did not disperse during 8 h. The packages *survival* and *coxme* of the open source program R v.3.2.2 (R Development Core Team 2015) were used. Selection regime was used as a fixed factor and block (replicate of the experiment) as random factor. Contrasts were assessed through joining of non-significant factor levels (Crawley 2007).

To investigate whether the selected lines showed a Milker-like or a Killer-like strategy we analyzed the dispersal rate of the predator during the interaction with its prey. Furthermore, theory predicts that the interaction period of the prey with the predator and the cumulative number of dispersing predators should differ as a consequence of these different dispersal strategies (van Baalen and Sabelis 1995). We therefore tested differences in these three parameters between selected lines and their controls. First, a MANOVA was applied to the dispersal rate (arcsine square root transformed), the interaction period and the cumulative number of dispersing predators combined, with selection regime and block as explanatory variables. After having found a significant difference between selected lines with the MANOVA, each parameter was tested separately.

Differences in the transformed (arcsine square root transformation) dispersal rate and the interaction period between lines were tested with a GLM with a Gaussian error distribution. To detect differences in the cumulative number of dispersing predators between lines, a GLM with a quasi-Poisson error distribution was applied.

RESULTS

Selection response experiment

The predators from the early-dispersal line dispersed significantly earlier than the predators from their control line ($\chi^2 = 7.5$, d.f. = 1, $P = 0.006$; FIGURE 3.1A). Similarly, the predators from the late-dispersal line stayed significantly longer on the leaf than the predators from their control line ($\chi^2 = 8.65$, d.f. = 1, $P = 0.003$; FIGURE 3.1B). These findings show that there is indeed a genetic component in the dispersal behavior of *P. persimilis*.

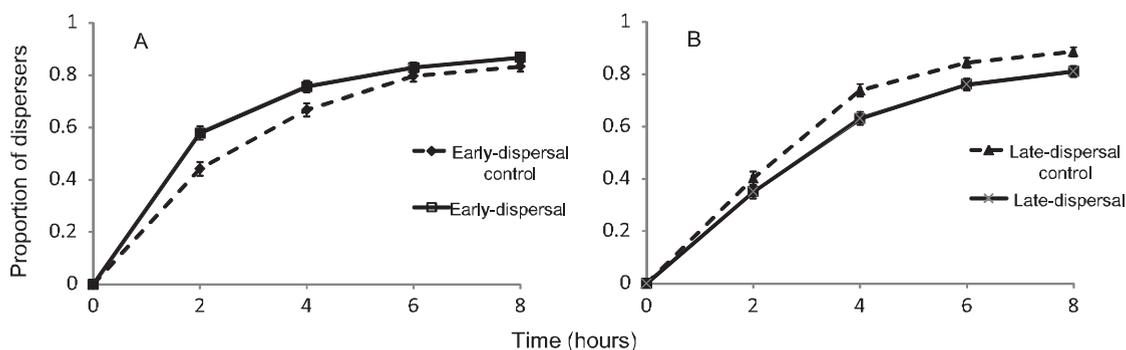


FIGURE 3.1 — Predatory mites respond to artificial selection on timing of dispersal. Panels show average proportions of dispersers (\pm SE) through time. A: The early-dispersal selection line and its control line; B: The late-dispersal selection line and its control line. Dashed line with rhombus: Early-dispersal-control line, Solid line with square: Early-dispersal line, Dashed line with triangle: Late-dispersal-control line, Solid line with cross: Late-dispersal line.

The two selection procedures were not performed exactly at the same time but in alternating weeks (see *selection procedure* in Materials and methods). Nevertheless, they were done under identical conditions in the same period, so we are convinced that the results were not affected by this slight asynchrony, hence, we also compared the two selection lines and the two control lines. The predators from the early-dispersal selection line dispersed significantly earlier than the late-dispersal selection line ($\chi^2 = 17.17$, d.f. = 1, $P < 0.001$). The two control lines did not differ from each other ($\chi^2 = 1.51$, d.f. = 1, $P = 0.22$).

Population dynamics experiment

We subsequently measured predator dispersal in a population-dynamical context (FIGURE 3.2). The two lines exploited the prey population in a different way: the early-dispersal line exploited the adult prey population much more slowly than the late-dispersal line and, as expected, initiated dispersal when there were still many adult prey on the leaf in comparison with the late-dispersal line, which initiated dispersal when the prey population was close to elimination (FIGURE 3.2).

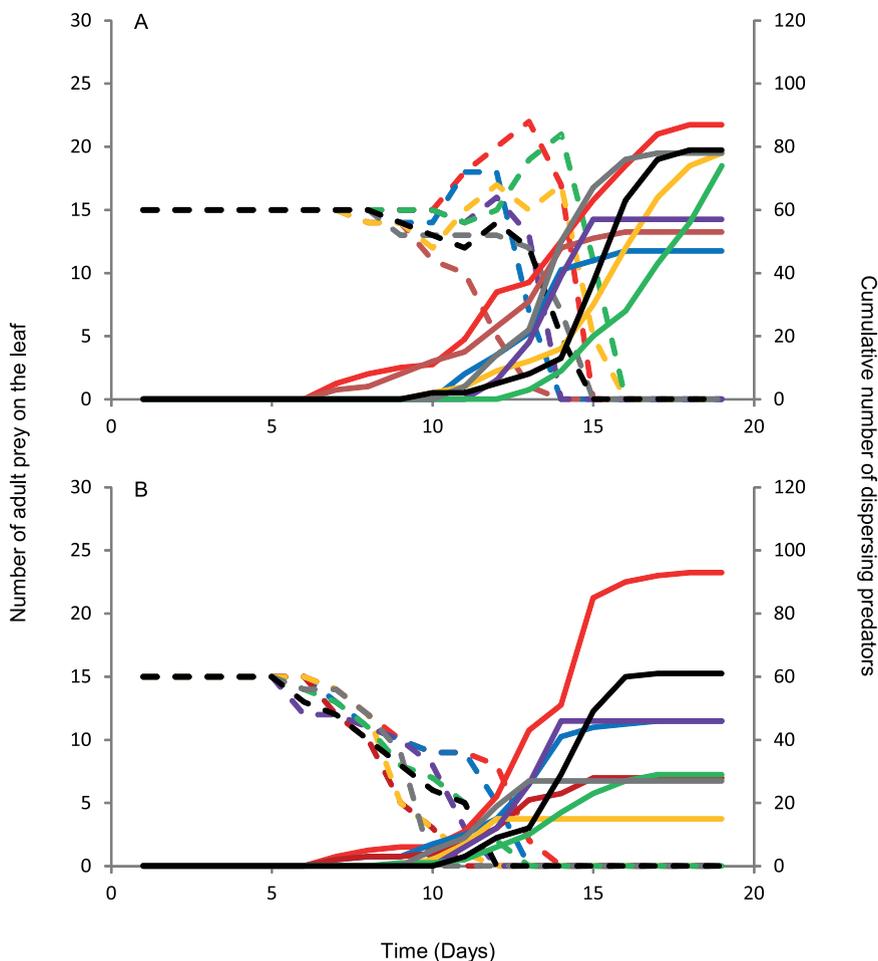


FIGURE 3.2 — Population dynamics of adult prey on the experimental leaf (dashed lines, left-hand vertical axis) and cumulative number of dispersing predators (solid lines, right-hand vertical axis). A: Early-dispersal selection line; B: Late-dispersal selection line. Different colors correspond to different replicates.

The combination of dispersal rate during the interaction period, interaction period and cumulative number of dispersing predators varied significantly between the selected lines as well as between blocks (MANOVA, Line: $F = 15.71$, d.f. = 1, $P < 0.001$, Block: $F = 7.01$, d.f. = 1, $P = 0.007$). Dispersal rate varied significantly between the selected lines (GLM: $\chi^2 = 0.02$, d.f. = 1, $P = 0.02$) and blocks (GLM: $\chi^2 = 0.04$, d.f. = 1, $P = 0.003$). The early-dispersal line had a significantly higher dispersal rate during the interaction period than the late-dispersal line (FIGURE 3.3A). In addition, the early-dispersal line interacted significantly longer with the prey (GLM: $\chi^2 = 25.00$, d.f. = 1, $P < 0.001$; FIGURE 3.3B) and produced significantly more dispersers than the late-dispersal line (GLM: $\chi^2 = 48.62$, d.f. = 1, $P = 0.04$; FIGURE 3.3C). These results show that it is possible to select for Milker-like and Killer-like predatory mite lines.

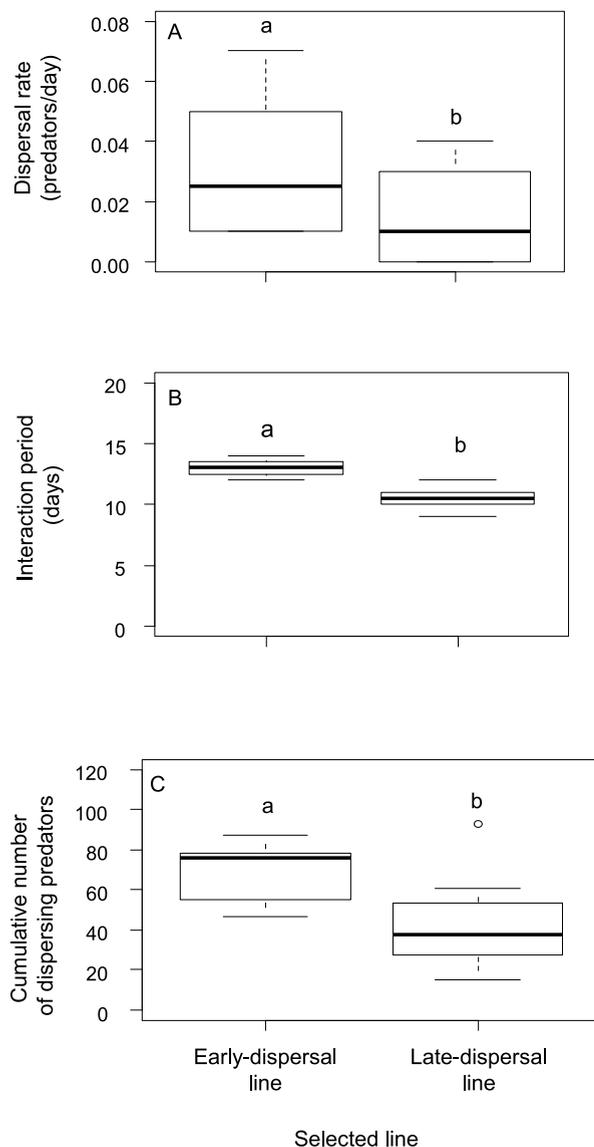


FIGURE 3.3 — Parameters from the two selected lines in the population dynamics experiment. A: the dispersal rate during prey exploitation (i.e., the time interval between predator introduction to the leaf and last day with at least three adult prey individuals on the leaf), B: the interaction period (i.e., the time interval between predator introduction to the leaf and prey elimination) and C: the cumulative number of dispersing predators (i.e., the total number of dispersers during the experiment). Boxes indicate the second and the third quartile; horizontal lines indicate the medians, whiskers above and below the box indicate the 90th and 10th percentiles. Different letters indicate significant differences ($N = 8$ for each line).

DISCUSSION

We found that it was possible to select for early and late aerial dispersal of the predatory mite *P. persimilis*, which supports the hypothesis that there is a genetic basis for the tendency to disperse aerially in *P. persimilis*. The population dynamics experiment showed that dispersal rates are intimately connected to patch exploitation strategies, with early dispersal (i.e., the so-called Milker strategy) from a prey patch resulting in prolonged predator-prey interactions on the patch and a higher total number of dispersing predators over the entire interaction period, and late dispersal (i.e., the so-called Killer strategy) resulting in a shorter interaction period and a lower number of dispersing predators. Hence, we selected for dispersal and show that this results in the predicted differences in dynamics on the prey patch.

Several studies show that dispersal behavior in *P. persimilis* and closely related phyto-seiid species is, to some extent, genetically determined and heritable (Jia et al. 2002; Maeda 2005; Nachappa et al. 2009). However, these studies focused on ambulatory dispersal, rather than dispersal by means of air currents. These modes of dispersal are fundamentally different in both the mechanisms that trigger them and their consequences: ambulatory dispersal is triggered by cues that indicate the nearby presence of prey (Mayland *et al.* 2000), whereas such cues suppress aerial dispersal (Sabelis and Afman 1994). Moreover, ambulatory dispersal always leaves the possibility to return to the point of departure, since it takes place within local populations (Sabelis et al. 2005). Aerial dispersal, in contrast, is passive, takes place among local populations at a metapopulation level (Sabelis et al. 2005), and it is virtually impossible for the predators to return to the departure point after dispersing because the distance that they have covered may be large and the wind direction should change exactly 180° between departure and return. In our study, the predators could not perceive the cues of the infested rose leaf, which served as a trap, because it was placed downwind from the prey patch, and they could not leave the leaf by walking because of the lanoline barrier at the bottom of the petiole. Hence the predators could only disperse by using the airflow in the wind tunnel and they could not return to the prey patch after they had departed. Our study thereby adds to the literature, showing that aerial dispersal in this species has a genetic basis.

The initiation of aerial dispersal might be stimulated or suppressed by a combination of cues, including the availability of prey and the density of competitors within a prey patch. However, other information may also play a role. For instance, if co-invasions by unrelated predators are not very frequent, kin-recognition (the ability to identify relatives) or social familiarity (the ability to identify individuals with which there was a prior association) may affect dispersal tendency. Several studies have reported that *P. persimilis* and other phyto-seiid species are able to distinguish related from non-related conspecifics (Faraji et al. 2000; Schausberger and Croft 2001) and socially familiar and unfamiliar conspecifics (Schausberger 2005, 2007; Zach et al. 2012; Muleta and Schausberger 2013) and adjust their behavior accordingly. In our study we used related (to some extent) and familiar individuals for the selection process, which are factors that can stimulate dispersal and can affect their dispersal tendency (Zach et al. 2012). Possibly there is genetic variation for the degree to which predatory mites adjust their dispersal tendency according to the presence of related conspecifics. Likewise, there may be genetic variation for the degree to which predatory

mites adjust their dispersal tendency according to chemical cues relating to the presence of prey in close proximity.

Better understanding of genetic heritability of traits relating to dispersal tendency and prey exploitation behavior in *P. persimilis* can contribute to our understanding of the evolution of alternative predator exploitation strategies. Furthermore, it can provide a basis for breeding programs to create strains with desirable traits for effective biological control. Because *P. persimilis* is commercially available as biological control agent of two-spotted spider mites, selecting for strains with desirable traits could improve the efficiency of managing spider mite pests. For instance, for the purpose of biological control of spider mites in ornamental crops, it is essential that predatory mites do not disperse before prey elimination. Hence, knowledge regarding the genetic heritability of traits related to dispersal behavior could potentially provide a basis for optimization of biological control programs.

Local population dynamics in metapopulations are often unstable and dispersal is therefore necessary for the global persistence of such predator-prey systems. Dispersal can also determine the exploitation strategy of predators: by dispersing earlier, predators can save prey for their offspring. When the local prey population grows, this offspring can produce more offspring, eventually resulting in a higher total number of dispersers from the patch. Yet, this prudent strategy can be invaded by predators with other, less prudent strategies, which consume the prey that was saved. Given that local populations may be more or less isolated, so the risk of invasions of prey patches by multiple predators varies, it is expected that there exists a continuum of strategies, ranging from prudent, milker strategies to selfish, killer ones. We show that it is possible to select for these strategies, confirming that such selection can also occur in nature. This is an important step in investigating the evolution of alternative prey exploitation strategies because it empirically demonstrates genetic heritability of the innate tendency to disperse aerially in *P. persimilis*, and it opens ways to experimentally investigate the consequences of these exploitation strategies, either alone or when played against each other.

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