



**UvA-DARE (Digital Academic Repository)**

**Should I stay or should I go?**

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

Revynthi, A.M.

[Link to publication](#)

*License*

**Other**

*Citation for published version (APA):*

Revynthi, A. M. (2017). *Should I stay or should I go? The role of dispersal and cannibalism in exploitation strategies of a predatory mite.*

**General rights**

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

**Disclaimer/Complaints regulations**

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

# 2

## Prey exploitation and dispersal strategies vary among natural populations of a predatory mite

A.M. Revynthi, M. Egas, A. Janssen & M.W. Sabelis

**ABSTRACT** — When predators commonly overexploit local prey populations, dispersal drives the dynamics in local patches, which together form a metapopulation. Two extremes in a continuum of dispersal strategies are distinguished: the ‘Killer’ strategy, where predators only start dispersing when all prey are eliminated and the ‘Milker’ strategy, in which predator dispersal occurs irrespective of prey availability. Theory shows that Milker strategies are not evolutionarily stable if local populations are well connected by dispersal. Using the predatory mite *Phytoseiulus persimilis*, we aim to investigate whether these two strategies occur in nature. We present a comprehensive survey of predator dispersal strategies using strains of *P. persimilis*, collected from 11 native populations from coastal areas in Turkey and Sicily. Using small wind tunnels, we measured dispersal rates and population dynamics of all populations in a system consisting of detached rose leaves, spider mites (*Tetranychus urticae*) as prey and *P. persimilis*. We found significant variation in the exploitation and dispersal strategies among predator populations. However, none of the collected strains showed the extreme Killer or Milker strategy. The results suggest that there is genetic variation for prey exploitation and dispersal strategies. Thus, different dispersal strategies in the Killer-Milker continuum may be selected for under natural conditions, which affects the predator-prey dynamics in local patches and is likely to determine persistence of the system at the metapopulation level.

## INTRODUCTION

Dispersal is a key process in population biology and ecology, influencing the persistence, distribution and abundance of populations as well as driving gene flow (Dunley and Croft 1990; Dingle 1996; Quinn et al. 2011). Decisions of individuals to disperse typically depend on local conditions such as the local density of conspecifics in the same patch (Otreron and Hanski 1983), food availability (Kuussaari et al. 1996), interspecific interactions (Weisser et al. 2001), sex ratio (Lawrence 1987, 1988; Colwell and Naeem 1999), kin recognition and kin interaction (Hamilton and May 1977), inbreeding avoidance (Greenwood 1980; Pusey and Wolf 1996), cannibalism (Pels 2001), individual personality (Quinn et al. 2011), temporal and spatial heterogeneity (Holt and Barfield 2001; Wiens 2001) and patch isolation (Conradt et al. 2001).

Dispersal affects various levels of biological organization, from an individual's fitness to population dynamics and community composition (Bowler and Benton 2005). Dispersal is particularly important when local populations are driven to extinction because of overexploitation, whereas persistence is observed at a metapopulation level due to continuous foundation of new local populations by dispersing individuals. Such dynamics occur, for example, when both predator and prey must disperse at a sufficient rate to balance local extinction with recolonization (Huffaker 1958; Taylor 1990; Janssen et al. 1997; Ellner et al. 2001). When individuals disperse from their patches at different time points, this creates asynchronous fluctuations in local abundance, which are a prerequisite for the persistence of metapopulations (Holyoak and Lawler 1996).

Whereas the role of dispersal in metapopulation persistence of systems characterized by local overexploitation received much attention, the effects of dispersal on local population dynamics are less well understood (Bowler and Benton 2009). The consequences of predator dispersal for the population dynamics of predators and prey were modelled by van Baalen and Sabelis (1995), who defined the so-called Milker-Killer dilemma, describing under which conditions these extremes of a continuum of dispersal strategies can evolve. Predators with the Killer strategy disperse only when the prey are eliminated. Under the Milker strategy, predators will disperse irrespective of prey density, thereby decreasing predation and allowing the prey population to produce more offspring. As a result, the predators' offspring will have more food, resulting in a longer interaction period of predators and prey on the patch. In contrast to the Killer strategy, the Milker strategy is a less selfish strategy (van Baalen and Sabelis 1995), in which the predators show a more prudent exploitative behavior. The Milker strategy is not evolutionarily stable because a local population of Milkermakers can be invaded by Killers, which have a reproductive benefit because they exploit the prey left behind by dispersing Milkermakers. When there is a low probability of invasion of Milker patches by Killers, the evolution of Milkermakers may be favored at the metapopulation level because the total number of offspring produced by a local population of Milkermakers is higher than that of Killers (van Baalen and Sabelis 1995; Pels 2001).

The Killer and Milker exploitation strategies differ in dispersal rate in presence of prey. Individuals of a Killer-type predator population do not disperse until the prey population is being exterminated, whereas Milker-individuals disperse early, long before prey elimination. Depending on the dispersal rate during the predator-prey interaction, three conse-

quences on the population dynamics of prey and predator are predicted. First, prey populations increase less when exploited by Killer predators than when exploited by Milker predators. Second, the local interaction period between a Killer predator population and its prey will be shorter than that of a Milker population. Third, local populations of Killer predators will produce less dispersing offspring over the entire local predator-prey interaction than Milker predators.

The formulation of the Milker-Killer dilemma was inspired by a study of plant-inhabiting mites, specifically the predatory mite *Phytoseiulus persimilis* Athias-Henriot and its prey, the phytophagous spider mite *Tetranychus urticae* Koch. This spider mite species occurs in local populations, which can be locally driven to extinction by their predators (Janssen and Sabelis 1992). These local populations are connected by predator dispersal (Janssen et al. 1997; Ellner et al. 2001). An experimental study investigated whether both dispersal strategies occur among predator strains of *P. persimilis* (Pels and Sabelis 1999), originally sampled from wild populations along the coast and inland on Sicily (Italy). Pels and Sabelis (1999) showed that all predator strains exterminated local prey populations, and the timing of dispersal appeared to have a genetic basis: one isofemale line derived from a coastal strain consistently showed dispersal close to or after prey elimination, whereas an isofemale line derived from an inland strain consistently dispersed long before all prey were eliminated. These behaviors were in line with Killer- and Milker-like strategies, respectively.

In their study, Pels and Sabelis (1999) did not replicate measurements of dispersal behavior of the strains. From their first measurements they chose two strains that showed the most extreme differences in dispersal behavior and created one isofemale line from each, which they used for further experiments. Thus, dispersal strategies were characterized only for two isofemale lines and hence, a thorough survey of predator dispersal behavior among natural populations is lacking. Also, quantifying the extent of variation in dispersal strategies from natural populations allows testing the predictions on the population dynamics of Killers and Milkers with their prey. We therefore returned to the Mediterranean area to collect natural populations of *P. persimilis* and measured their dispersal characteristics using local populations in a laboratory set-up, similar but more accurate than that of Pels and Sabelis (1999). We aim to quantify the extent of variation in dispersal strategies by estimating dispersal rates in the presence of prey, and to test the predicted consequences of dispersal for the population dynamics of predators and prey.

## **MATERIALS AND METHODS**

### ***Collection of predatory mites***

*Phytoseiulus persimilis* was collected from fields in Turkey in 2013 and in Sicily in 2014. These locations were chosen because natural populations of this predator occur there and it was not introduced as a biological control agent. Upon spotting the predators in spider-mite colonies, infested leaves with prey and predators were transferred inside plastic bottles that were closed and had an air inlet covered with mite proof gauze (80  $\mu$ m).

In Turkey, samples were collected from six sites in the region of Hatay (36°04.950'N, 35°56.728'E) and Erdemli (36°36.267'N, 34°15.926'E) (FIGURE 2.1). In Hatay, predators were collected from Samandağ, Koyunoğlu, Kuşalanı, Karaçay and Uzunbağ; in Erdemli from

Kocahasanlı. Predatory mites were found on cucumber (*Cucumis sativus*), bean (*Phaseolus vulgaris*) and eggplant (*Solanum melongena*). In Erdemli, predators were also collected from the weed *Tribulus terrestris*. All host plants were infested with spider mites (*T. urticae*).

Predators were also collected from the western part of Sicily (38°02.573'N, 12°59.747'E) at five sites: Castelvetroano, Alcamo, Palermo, Trabia and Lascari (FIGURE 2.1). Natural populations of *P. persimilis* occurred on spider-mite infested melon (*Curcubita pepo*) and castor bean plants (*Ricinus communis*) and on spider-mite infested weeds of *Convolvulus* sp.

All sampling sites, in both locations, where the mites were collected, were along the coast. We visited inland sites (approx. 50 km away from the coast), but we did not manage to find and collect predators.

### Laboratory cultures

Rose plants (*Rosa* sp. var. Avalanche) were provided by Olij Rozen and were allowed to grow in a climate room (25 °C, 70% RH, 16L:8D) free of herbivores. Lima bean plants (*Phaseolus lunatus* L.) were grown from seeds in a climate room (25 °C, 60% RH, 16L:8D) free of herbivores.

The *T. urticae* strain used to feed the predators was originally collected from cucumber plants in a commercial greenhouse in May 1994 (Pallini et al. 1997), and was reared on Lima beans (*P. lunatus*) in a climate room (26 °C, 60% RH, 16L:8D).

The predatory mite strains were reared on spider-mite infested Lima bean leaves in a walk-in climate room at 25 °C, 70% RH and 16L:8D. We used the same closed rearing system as Pels and Sabelis (1999), consisting of a plastic float inside a plastic tray, which was

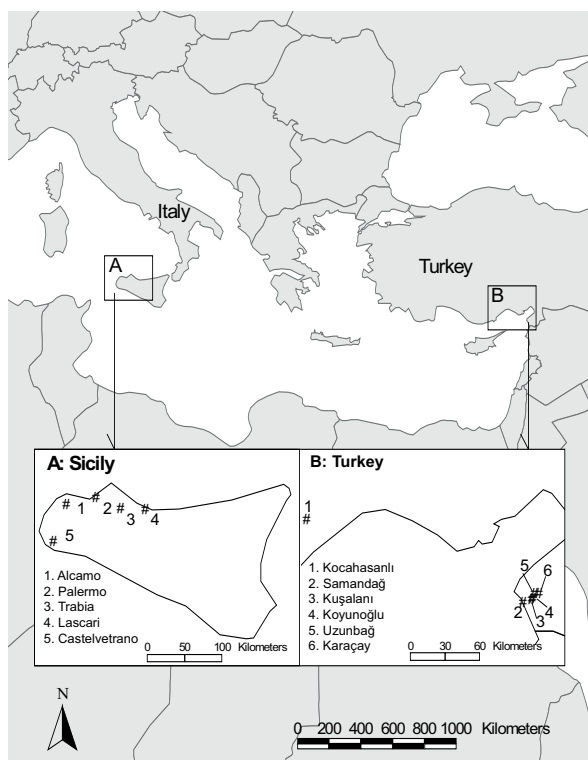


FIGURE 2.1 — Map showing the sample sites of populations of the predatory mite *Phytoseiulus persimilis*.

filled with a 15-mm layer of water with dissolved soap. Three times per week, two bean leaflets infested with spider mites were placed on the float, which provided the predators with sufficient food. In order to allow the mites to disperse ambulatorily without drowning, the plastic float was covered with a plastic aquarium (19.5 × 13.0 × 11.5 cm) with a piece of fine-meshed gauze hanging from the ceiling, touching the float/leaflets. For ventilation, a rectangular hole was made in the ceiling of the aquarium, covered with fine meshed gauze (80 µm).

### ***Sequencing of COI and ITS genes***

To identify the collected strains to the species level, the mitochondrial cytochrome oxidase I (COI) gene and the internal transcribed spacer (ITS) gene were sequenced. DNA was extracted from single adult females of *P. persimilis* with the Chelex maceration method (Walsh et al. 1991). Five mites per strain were used for the DNA extraction and were introduced individually in 0.5 ml tubes containing 100 µl of 5% Chelex 100 (Biorad Chelex 100, Richmond, CA, USA). The samples were incubated at 56 °C with 5 µl of proteinase-K for 60 min and were then heated for 10 min at 95 °C. They were stored in the freezer at -20 °C.

The mitochondrial COI region was amplified using the 5'GGTCAACAAATCATAAA GATATTGG3' (forward) and 5'TAAACTTCAGGGTGACCAAAAATCA3' (reverse) primers (Jørgensen et al. 2007). The primers that were used for amplifying the nuclear ITS region were 5'AGAGGAAGTAAAAGTCGTAACAAG3' (forward) and 5'ATATGCT TAAATTCAGGGGG3' (reverse) (Navajas et al. 1999). For the PCR, we used 25 µl reaction volumes containing 13.3 µl water, 2.5 µl of 10 × Buffer (HT BioTechnology, Cambridge, UK), 0.5 µl Super Taq polymerase (5 U/µl), 2.5 µl dNTP's, 1.2 µl BSA, 0.5 µl of each primer and 4 µl of DNA sample. For COI, samples were preheated at 94 °C for 2 min, 35 cycles of denaturation at 94 °C for 10 s, annealing at 48 °C for 30 s and amplification at 72 °C for 55 s, and a final extension step at 72 °C for 10 min (Jørgensen et al. 2007). For ITS, samples were denatured at 94 °C for 4 min and then PCR was carried out for 30 cycles of 1 min denaturation at 93 °C, 1 min annealing at 50 °C and 1 min extension at 72 °C (Navajas et al. 1999). The PCR products were visualized with UV light using a 1.5% agarose gel stained with ethidium bromide. Direct sequencing of PCR amplifications were done by MacroGen EZ-seq service, using the same primers as for the PCR. The sequences were read and compared using the CLC Genomics workbench 3 (Qiagen, CLC Bio).

### ***Dispersal experiments***

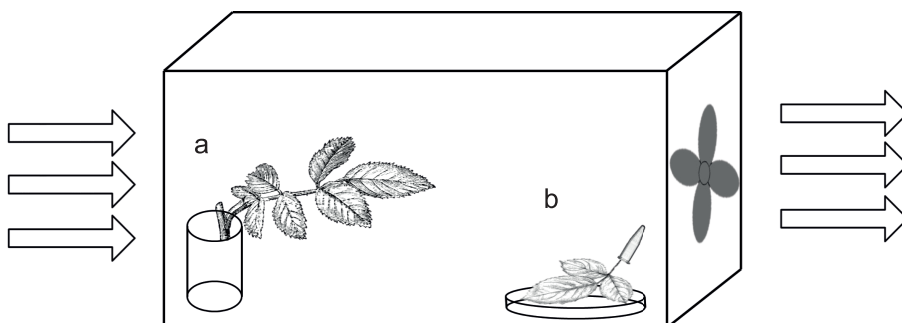
To measure dispersal, we used wind tunnels similar to those of Pels and Sabelis (1999). They consisted of a plastic aquarium (25.3 × 15.8 × 15.5 cm) with two holes on the short sides (11.5 cm diameter each) covered with mite-proof gauze (80 µm). The aquarium was closed with a glass lid and sealed with Parafilm. A fan was placed close to one hole, causing an air flow of 0.4 m/s inside the aquarium (FIGURE 2.2).

Initially, Lima bean (*P. lunatus*) was used as a host. However, the leaves wilted within 24 h after being cut. We therefore used rose leaves, which could be preserved for a long period without suffering from water stress. Rose leaves with a shoot of ca. 5 cm were cut and the shoots were inserted in a small vial (24.5 mm diameter, 40 mm height) filled with wet floral foam (Oasis) to maintain leaf turgidity. A thick layer of lanolin was applied to the base of the petiole to prevent mites from escaping. Fifteen 2-day-old adult female spider mites

were introduced on the leaf and were allowed to feed and oviposit for two days. Missing females were replaced daily during these two days. After 48 h, one 2-day-old mated adult female predatory mite was introduced on the leaf, which was then placed with the vial at the upwind side in the wind tunnel. Predatory mites that dispersed aurally from the leaf using the air flow through the wind tunnel landed somewhere inside the wind tunnel. In order to capture them, we introduced a Petri dish with a young, spider-mite infested rose leaf as a trap, located on the downwind side on the bottom of the wind tunnel. The infested rose leaf also had a ca. 3 cm shoot, which was inserted through a hole in the lid of an Eppendorf tube (1.5 ml) filled with wet floral foam, providing it with the necessary moisture. The tube was sealed with Parafilm (FIGURE 2.2). After introduction of the predator, the numbers of adult prey and adult predators on the leaf, on the trap, on the cover and elsewhere in the wind tunnel were assessed every 24 h. The experiment ended when there were no prey and predators left on the leaf. The experiment was repeated 5× for each strain in a climate room at 25 °C, 70% RH and 16L:8D.

Per country of origin, the strains were tested simultaneously, using six wind tunnels in one climate room. A line derived from mites of Koppert Biological Systems (Berkel en Roderijs, the Netherlands) was tested together with the Sicilian strains. This line has been maintained in our laboratory for many years and was used to get an indication of the dispersal behavior of this laboratory population.

To characterize a strain in the continuum from Milker to Killer, we analyzed three parameters: the dispersal rate of the predator during the interaction period, the interaction period of the predators and prey and the cumulative number of dispersing predators. To calculate the predator dispersal rate during the predator-prey interaction, we first calculated the proportion of dispersers of the total number of predators in the wind tunnel for each day of the interaction, and then averaged these daily proportions. Because all predators will disperse towards the end of the interaction period due to lack of prey, irrespective of their exploitation strategy, we excluded the last part of the interaction period, limiting it from the day of predator introduction until the last day, with at least three adult prey individuals on the leaf. The interaction period was taken as the time interval between predator introduction and prey elimination, i.e., the day when there were no more prey on the leaf. The cumulative number of dispersing predators was taken as the total number of predators that dispersed from the leaf during the entire interaction period and until the end of the experiment.



**FIGURE 2.2** — Wind tunnel, consisting of a plastic aquarium with two holes covered with mite-proof gauze and a fan connected to one of them. a: Rose leaf, where the prey and predator were released, and b: trap with spider-mite infested rose leaf. Arrows indicate the direction of the air current.

Specifically, we aimed at finding significant differences among strains with respect to the three parameters, with Milker-like strains showing a higher dispersal rate during the predator-prey interaction, having a longer interaction period with the prey and producing a higher cumulative number of dispersers than Killer-like strains.

All statistical analyses were performed with R v.3.0.1 (R Development Core Team 2012). A MANOVA was applied to the dispersal rate (arcsine transformation), the interaction period and the cumulative number of dispersing predators combined, with strain and time in culture as explanatory variables. Time in culture is the number of weeks since the start of the predator culture, and was included to verify whether culturing the predators in the laboratory resulted in changes in their exploitation strategy (see TABLE S2.1). After having found a significant difference among strains with the MANOVA, each parameter was tested separately.

Differences in the arcsine-transformed dispersal rate among strains were tested with a GLM with a Gaussian error distribution. For differences in the interaction period a GLM with Gaussian error distribution was used and differences in the cumulative number of dispersing predators among strains were assessed with a GLM with quasi-Poisson error distribution. Contrasts were made by joining the non-significant factor levels (Crawley 2007).

After the first replicate with the Turkish strains, we started keeping a detailed record of the number of predators present on the leaf through time. With these numbers and the number of dispersed individuals, we estimated the population growth rate  $\gamma$  of each strain:

$$\gamma = [\ln(P_t / P_0) / t] + \mu,$$

where  $P_t$  is the predator population size at time  $t$ ,  $P_0$  is the initial predator density,  $\mu$  is the dispersal rate (estimated as described above),  $t$  is the time from the day when the predator was introduced on the leaf until the last day with at least three adult prey individuals on the leaf (Diekmann et al. 1988; van Baalen and Sabelis 1995). Differences in population growth rates among strains were tested with a GLM with a Gaussian error distribution.

## RESULTS

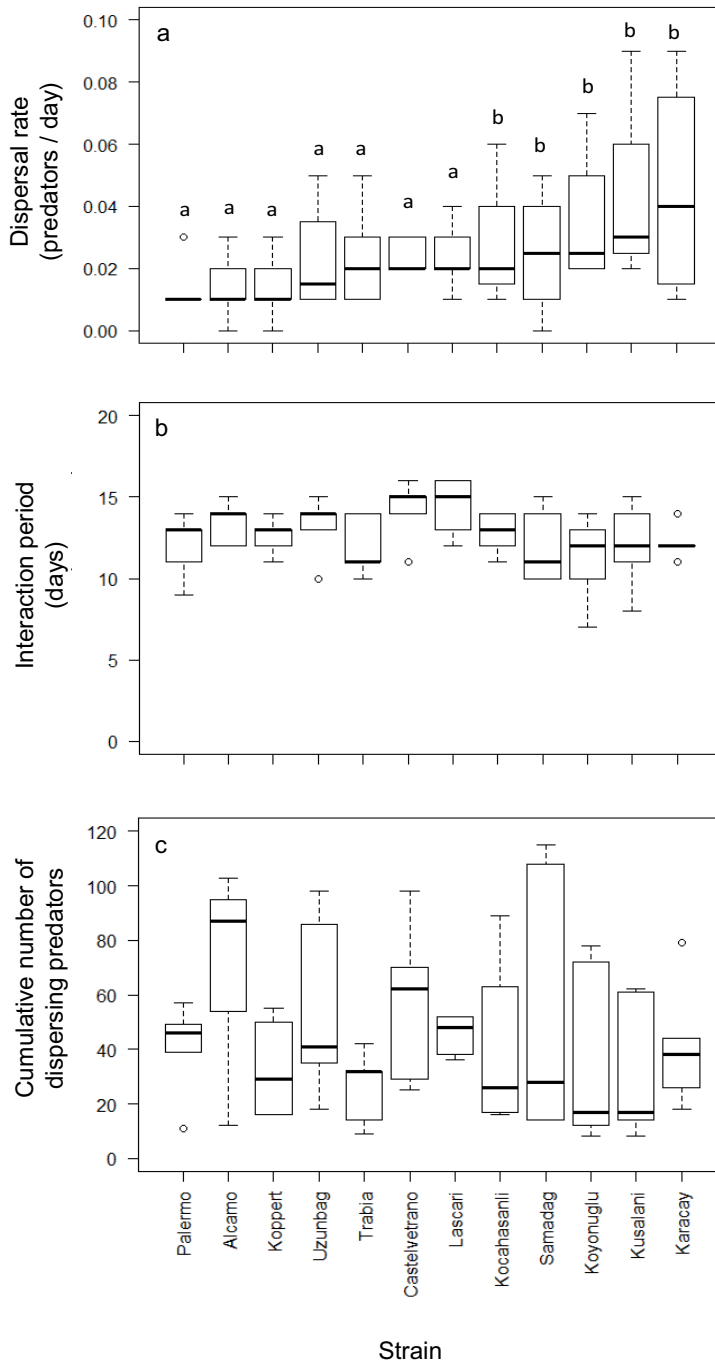
### *Sequencing of the COI and ITS genes*

The sequences of both COI and ITS genes showed that the mites belonged to the species *P. persimilis*. All strains, including the Koppert line, had a COI sequence identical to the KF966638 entry in GenBank and an ITS sequence identical to the HQ404818 entry (Tsolakis et al. 2012).

### *Dispersal experiments*

The combination of dispersal rate during the interaction period, interaction period and cumulative number of dispersing predators varied significantly among strains as well as with the time in culture and their interaction (MANOVA, Strain:  $F = 1.82$ , d.f. = 90,  $P = 0.01$ , Time in culture:  $F = 8.07$ , d.f. = 28,  $P < 0.001$ , Strain  $\times$  Time in culture:  $F = 1.70$ , d.f. = 90,  $P = 0.03$ ). Dispersal rates varied significantly among strains (GLM: deviance = 0.005, d.f. = 11,  $P = 0.03$ ), with time in culture (GLM: deviance = 0.001, d.f. = 1,  $P = 0.03$ ), as well as with their interaction (GLM: deviance = 0.009, d.f. = 11,  $P = 0.001$ ). The strains Palermo, Alcamo, Koppert, Uzunbağ, Trabia, Castelvetrano and Lascari, had significantly



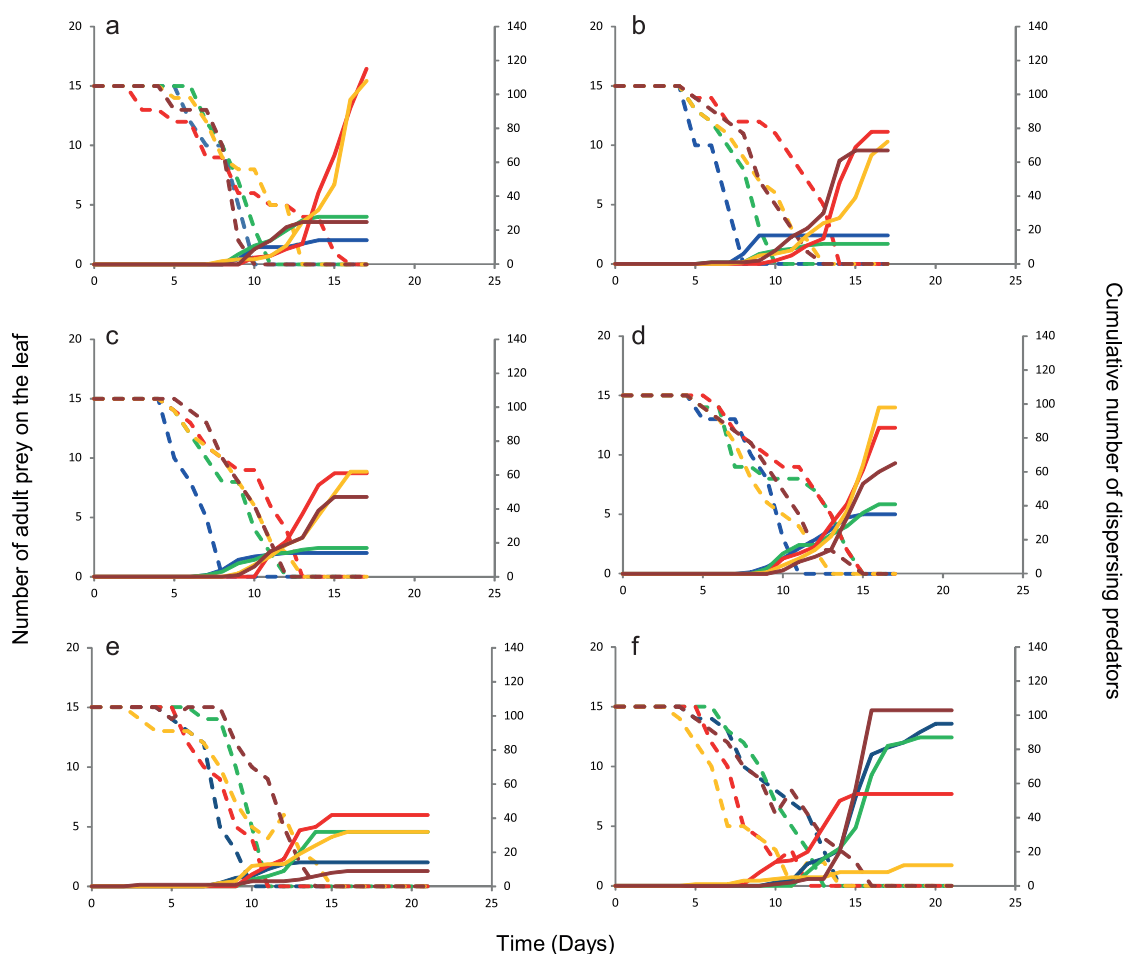


**FIGURE 2.3** — Parameters of the predator-prey (*Phytoseiulus persimilis* – *Tetranychus urticae*) population dynamics experiments used to characterize all strains in the Milker-Killer continuum. a: Dispersal rate during the interaction period (i.e., the time interval between predator introduction until a maximum of three adult prey were present). b: Interaction period (i.e., the time interval between predator introduction and prey elimination). c: The cumulative number of dispersing predators (i.e., the total amount of dispersers during the experiment). Boxes indicate the second and the third quartile, horizontal lines separating the boxes indicate the medians (N = 5), whiskers above and below the box indicate the 90th and 10th percentiles. Different letters indicate significant differences (contrasts after GLM,  $P < 0.05$ ).

lower dispersal rates than the strains Kocahasanlı, Samandağ, Koyunoğlu, Kuşalanı and Karaçay (deviance = 0.01, d.f. = 2,  $P < 0.001$ ; FIGURE 2.3a).

There was variation in the dynamics of the prey and predators among replicates and strains (FIGURES 2.4, S2.1 and S2.2). In all cases, predators initiated dispersal while there were still prey present on the leaf, yet the interaction period, i.e., the time between predator introduction and prey elimination, was not significantly different among strains (GLM: deviance = 51.73, d.f. = 11,  $P = 0.16$ ; FIGURE 2.3b). The interaction period increased significantly with time in culture (GLM: deviance = 33.38, d.f. = 1,  $P = 0.002$ ).

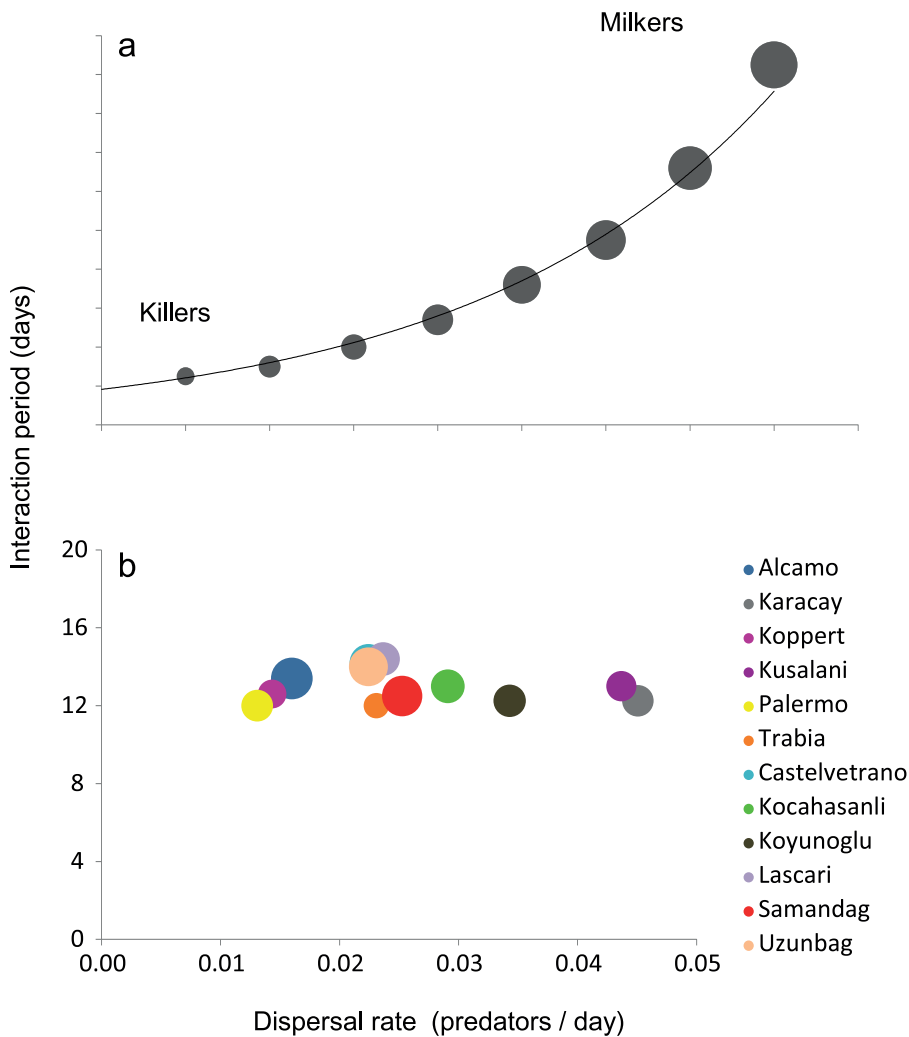
Differences in dispersal rates did not result in significant differences in the cumulative number of dispersing predators among strains (GLM: deviance = 195.0, d.f. = 11,  $P = 0.52$ ; FIGURE 2.3c). Of all collected strains, the one from Alcamo produced the highest number of dispersers and that of Trabia the lowest ( $70.2 \pm 16.8$  and  $25.8 \pm 6.2$  individuals on average, respectively).



**FIGURE 2.4** — Predator-prey (*Phytoseiulus persimilis* – *Tetranychus urticae*) population dynamics in the wind tunnel experiments. Shown are the adult prey on the leaf (dashed lines, left-hand axis) and cumulative number of dispersing predators (solid lines, right-hand axis). The presented strains demonstrate the variation in prey exploitation and cumulative number of dispersers in every replicate. a: Samandağ, b: Koyunoğlu, c: Kuşalanı, d: Uzunbağ, e: Trabia, f: Alcamo. Blue: replicate 1, green: replicate 2, red: replicate 3, orange: replicate 4 and purple: replicate 5. For the population dynamics of all strains see FIGURES S2.1 and S2.2.

According to the Milker-Killer concept, the interaction period should be positively related to the dispersal rate during the interaction period and the cumulative number of dispersers. We found little evidence for this (FIGURE 2.5). Even though there was no significant variation regarding the interaction period among strains, Alcamo, Koppert and Palermo strains showed a tendency towards the Killer strategy, whereas Kuşalanı and Karaçay showed a tendency towards the Milker strategy.

The population growth rates did not differ significantly among the strains (GLM: deviance = 0.02, d.f. = 11,  $P = 0.96$ ) (see TABLE S2.2). On average, the growth rate was 0.39 for the Turkish strains, 0.38 for the Sicilian strains and 0.42 for the Koppert strain.



**FIGURE 2.5** — The relation between interaction period, dispersal rate during the interaction period, and cumulative number of dispersers. The size of each dot represents the average cumulative number of dispersing predators. a: Theoretical prediction based on the model proposed by van Baalen and Sabelis (1995) and b: results from the tested *Phytoseiulus persimilis* strains; different colors represent different strains. Strains with more Killer-like dispersal strategy have a low dispersal rate, a short interaction period and low cumulative numbers of dispersing predators, hence, they are expected to appear on the lower left side of the graph and have a smaller dot. Strains with a more Milker-like dispersal strategy are expected in the top right side of the graph and with a larger dot.

## DISCUSSION

Earlier work showed first evidence for the existence of variation in exploitation strategies of the predatory mite *P. persimilis*, one isofemale line resembling the Killer strategy in which predators start dispersing at prey depletion, the other isofemale line resembling the Milker strategy in which predators start dispersing before prey elimination, leaving food for their offspring (Pels and Sabelis 1999). Here, we aimed to investigate whether the Killer and the Milker strategies occur in nature using strains derived from native populations. We used dispersal rate during the predator-prey interaction as a criterion to determine which exploitation strategy the predators employ. Our results showed significant variation in dispersal rate across the strains (FIGURE 2.3a). The strains Palermo, Alcamo, Koppert, Uzunbağ, Trabia, Castelvetro and Lascari had lower dispersal rates, and therefore we conclude that they employ a more Killer-like dispersal strategy, than the strains of Kocahasanlı, Samandağ, Koyunoğlu, Kuşalanı and Karaçay that employ a more Milker-like dispersal strategy. Given the differences in the dispersal rates, we expected to observe the predicted consequences for the predator-prey dynamics and the cumulative number of dispersers; however, this was not the case. Higher dispersal rates did not result in an increase in prey population, a prolonged interaction period and a higher production of dispersers, thus we conclude that none of the strains we collected showed an extreme Killer or Milker strategy. Our results show variation in exploitation strategies ranging from a more Killer-like to a more Milker-like strategy.

Given that the variation in dispersal rates did not result in the expected consequences on the population dynamics of the prey and predator, other characteristics, such as population growth rate might also vary with strain (cf. dispersal syndromes; Stevens et al. 2013, 2014). Predator populations with high growth rate develop faster and exploit the prey patch more rapidly than populations with lower growth rate. As a result the interaction period is shorter and the cumulative number of dispersers produced over the interaction time is smaller. Therefore, we also estimated population growth rates from the data. The Turkish strains seemed to exhibit a slightly higher growth rate than the Sicilian strains (see TABLE S2.2), however, the variation in the population growth rate among the strains was not significant. This implies that the lack of population dynamical response to variation in dispersal rate is not due to variation in population growth rate.

The population dynamics may of course also vary with prey characteristics such as prey dispersal and anti-predation strategies. If the prey mites respond flexibly to predation pressure, the predator exploitation strategy might not have much net effect on the interaction period and the cumulative number of predator dispersers. In predator-prey interactions, it is to be expected that prey disperse as well, either to avoid predation or to find a better host plant. Milker-Killer-like strategies may occur in spider mites exploiting their host plant as well; spider mites also overexploit their food source, and Killer-like predator exploitation selects for higher prey dispersal (Sabelis et al. 2002). Even though dispersing prey were never observed in the wind tunnels, we cannot exclude the possibility that more prey dispersed from the arena to the trap in replicates with Killer-like predator strains, and the setup of the wind tunnels did not allow for observations on anti-predator behavior. If the interaction period is also dependent on such condition-dependent prey behavior, it is still an open question what would be the best exploitation strategy for the predators.

We tried to maintain the natural variation in dispersal behavior of the predators in the laboratory by using closed rearing units, which allowed the predators to leave the prey patch, but to which they could subsequently return. The mites were collected from the field and subsequent adaptation to the rearing conditions might have affected their dispersal behavior. Indeed, we found that the longer the predators had been kept in the laboratory, the longer became the interaction period and the lower their dispersal tendency. Mites collected from the field tend to be more active (personal observation), hence this is another reason why time in culture was chosen as an explanatory variable (see TABLE S2.1). Furthermore, animals are known for changing their dispersal behavior and increase their dispersal rates in response to translocation (Pettit et al. 2016).

Genetic variation among predators within each strain may also contribute to variation among replicates. In contrast to Pels and Sabelis (1999), we did not conduct the experiments with isofemale lines but tested one family in each replicate (each experiment was started with one adult female predator). The experiments of Pels and Sabelis (1999) show much less variation in interaction time among replicates than the experiments reported here, suggesting that there was genetic variation for prey exploitation within the strains studied here. The variation found among strains in this study suggests that there is a genetic component for dispersal tendency in the presence of prey, but the question remains to what extent this variation is heritable. To test this, selection should be performed for Milker and Killer lines of predators.

In the current study, we did not observe the population dynamical consequences predicted by the model of van Baalen and Sabelis (1995). We suggest that the discrepancy is due to the model assumption of a fixed dispersal probability during the interaction period; dispersal likely depends on the condition of the individual (Kisdi et al. 2012) and its environment (Clobert et al. 2009). It remains to be investigated how these factors affect dispersal behavior. In our experiment, dispersal was probably affected by predator density and food availability. All predators from all strains and in all replicates started dispersing close to, but still before prey elimination. The predators that initiated dispersal were all adults, mostly females. Females need much more food to reproduce than nymphs need to become adult (Sabelis 1981). Hence, when there is no longer enough food for adult females to reproduce, it might be more profitable for them to disperse. The small amount of food left behind is probably enough for many nymphs to become adult and disperse later. Hence, there may be a relation between the stage structure of the population and the dispersal behavior.

The Milker-Killer dilemma is broadly applicable to predator-prey systems that are characterized by local overexploitation and metapopulation dynamics, typical for many arthropod predator-prey systems (Hassell 1978). Analogies may also be found in parasitoid-host systems. We can hypothesize that parasitoids that do not kill their host immediately, i.e., koinobiont parasitoids, may have alternative exploitation strategies. By adopting a prudent exploitation strategy, the parasitoid larvae developing in the host allow the host to increase in body mass. This exploitation strategy can be evolutionary stable only when the host is parasitized by one adult. Superparasitism of the same host will select for more selfish exploitation strategies adopted by the parasitoid larvae, since co-exploitation will induce competition for food. We are not aware, however, of experimental evidence for the above

hypothesis. The hymenopterous parasitoid *Pachycrepoideus vindemmiae* can be considered as a suitable candidate to test it because female parasitoids of this species appear to vary the number of eggs deposited in a host depending on the number of conspecifics exploiting the same patch with hosts (Goubault et al. 2005). Another example of analogy is host infection by pathogens (van Baalen and Sabelis 1995; Sabelis et al. 2002). In the same way that a predator can drive local prey to extinction rapidly or slowly, a pathogen can reproduce fast in its host, thereby decreasing the host's longevity, or it can reproduce more slowly without affecting the longevity of its host much. This results in a continuum ranging from extreme virulence to extreme avirulence (van Baalen and Sabelis, 1995; Sabelis et al., 2002).

Dispersal is generally treated as a phenomenon that is either only genetically determined and linked to life-history traits (e.g., Stevens et al. 2013, 2014) or plastic and dependents on context (e.g., Clobert et al. 2009; Bitume et al. 2013, 2014). However, for a comprehensive understanding of dispersal, both perspectives need to be brought together (Bonte and Dahirel 2016). As explained above, dispersal behavior in our strains of *P. persimilis* also appears to depend on the individual state and its environment, but the significant variation in dispersal rate among strains encountered here suggests a genetic component (see also Jia et al. 2002). This in turn suggests that it is possible to select for lines with more Killer-like or more Milker-like strategies. Creating such lines would provide an important tool for further studies of the evolution and maintenance of variation in prey exploitation strategies and their effects on local and global population dynamics.

**ACKNOWLEDGEMENTS** — This paper is dedicated to the memory of MW Sabelis, who passed away on the 7th of January 2015. We thank C Kazak, I Doker, S Ragusa and H Tsolakis for helping with the sampling in Turkey and Sicily. We also thank CA Villarroel and JM Alba for helping with the analysis of the sequences and JA Pascual, JM Campo for helping design the map, F Faraji for help with the identification of the predatory mites and P de Ruiters for constructive comments on the manuscript.

## REFERENCES

- Bitume E V, Bonte D, Ronce O, et al. (2013) Density and genetic relatedness increase dispersal distance in a subsocial organism. *Ecol Lett* 16:430–437.
- Bitume E V, Bonte D, Ronce O, et al. (2014) Dispersal distance is influenced by parental and grandparental density. *Proc. R. Soc. London B Biol. Sci.* 281.
- Bonte D, Dahirel M (2016) Dispersal: a central and independent trait in life history. *Oikos* 126: 472–479.
- Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behavior to spatial dynamics. *Biol Rev Camb Philos Soc* 80:205–225.
- Bowler DE, Benton TG (2009) Variation in dispersal mortality and dispersal propensity among individuals: the effects of age, sex and resource availability. *J Anim Ecol* 78:1234–1241.
- Clobert J, Le Galliard J-F, Cote J, et al (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol Lett* 12:197–209.
- Colwell RK, Naeem S (1999) Sexual Sorting in Hummingbird Flower Mites (Mesostigmata: Ascidae). *Ann Entomol Soc Am* 92:952–959.
- Conradt L, Roper TJ, Thomas CD (2001). Dispersal Behavior of Individuals in metapopulations of Two British Butterflies. *Oikos* 95: 416–424
- Crawley MJ (2007) *The R Book*, John Wiley & Ltd., Chichester.
- Diekmann O, Metz JA, Sabelis MW (1988) Mathematical models of predator/prey/plant interactions in a patch environment. *Exp Appl Acarol* 5:319–342.
- Dingle H (1996) *Migration: The Biology of Life on the Move*, Oxford Univ. Press, USA.

- Dunley JE, Croft BA (1990) Dispersal between and colonization of apple by *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acarina: Phytoseiidae). *Exp Appl Acarol* 10:137–149.
- Ellner SP, McCauley E, Kendall BE, et al (2001) Habitat structure and population persistence in an experimental community. *Nature* 412:538–543.
- Goubault M, Outreman Y, Poinsot D, Cortesero AM (2005) Patch exploitation strategies of parasitic wasps under intraspecific competition. *Behav Ecol* 16:693–701.
- Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162.
- Hamilton WD, May RM (1977) Dispersal in stable habitats. *Nature* 269:578–581.
- Hassell MP (1978) Arthropod predator-prey systems. Princeton University Press, Princeton, NJ, USA.
- Holt RD, Barfield M (2001) On the relationship between the ideal free distribution and the evolution of dispersal. In: Clobert J., Danchin E., Dhondt A.A., Nichols J.D. (eds), *Dispersal*. Oxford Univ. Press, New York, pp 83–95
- Holyoak M, Lawler SP (1996) Persistence of an Extinction-Prone Predator-Prey Interaction Through Metapopulation Dynamics. *Ecology* 77:1867.
- Huffaker C (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27: 343–383.
- Janssen A, Sabelis MW (1992) Phytoseiid life-histories, local predator-prey dynamics, and strategies for control of tetranychid mites. *Exp Appl Acarol* 14:233–250.
- Janssen A, van Gool E, Lingeman R, et al (1997) Metapopulation dynamics of a persisting predator-prey system in the laboratory: time series analysis. *Exp Appl Acarol* 21:415–430.
- Jia F, Margolies DC, Boyer JE, Charlton RE (2002) Genetic variation in foraging traits among inbred lines of a predatory mite. *Heredity* 89:371–379.
- Jørgensen A, Møbjerg, N, Kristensen RM (2007) A molecular study of the tardigrade *Echiniscus testudo* (Echiniscidae) reveals low DNA sequence diversity over a large geographical area. *J Limnol* 66:77.
- Kisdi E, Utz M, Gyllenberg M (2012) Evolution of condition-dependent dispersal. In: Clobert J, Bagnette M, Benton T, Bullock JM, (eds), *Dispersal Ecology and Evolution*. Oxford Univ. Press, New York, pp 139–151.
- Kuussaari M, Nieminen M, Hanski I (1996) An experimental study of migration in the Glanville Fritillary butterfly *Melitaea cinxia*. *J Anim Ecol* 65: 791–801.
- Lawrence WS (1987) Dispersal: an alternative mating tactic conditional on sex ratio and body size. *Behav Ecol Sociobiol* 21:367–373.
- Lawrence WS (1988) Movement Ecology of the Red Milkweed Beetle in Relation to Population Size and Structure. *J. Anim. Ecol.* 57:21–35.
- Navajas M, Lagnel J, Fauvel G, Moraes G De (1999) Sequence variation of Ribosomal Internal Transcribed Spacers (ITS) in commercially important Phytoseiidae mites. *Exp Appl Acarol* 23:851–859.
- Otronen, M, Hanski I (1983) Movement Patterns in *Sphaeridium*: Differences between Species, Sexes, and Feeding and Breeding Individuals. *J. Anim. Ecol.* 52: 663–680.
- Pallini, A, Janssen A, Sabelis MW (1997) Odour-mediated responses of phytophagous mites to conspecific and heterospecific competitors. *Oecologia*. 110:179–185.
- Pels B, Sabelis MW (1999) Local dynamics, overexploitation and predator dispersal in an acarine predator-prey system. *Oikos* 86: 573–583.
- Pels B (2001) Evolutionary Dynamics of Dispersal in Predatory Mites. PhD dissertation, Faculty of Science, University of Amsterdam, Amsterdam, the Netherlands.
- Pettit LJ, Greenlees MJ, Shine R (2016) Is the enhanced dispersal rate seen at invasion fronts a behaviorally plastic response to encountering novel ecological conditions? *Biol. Lett.* 12(9): 20160539.
- Pusey A, Wolf M (1996) Inbreeding avoidance in animals. *Trends Ecol Evol* 11:201–206
- Quinn JL, Cole EF, Patrick SC, Sheldon BC (2011) Scale and state dependence of the relationship between personality and dispersal in a great tit population. *J Anim Ecol* 80:918–928.

- R Development Core Team. (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Sabelis, M.W. (1981) Biological control of two-spotted spider-mites using phytoseiid predators. Part I. PhD dissertation, Department of Entomology, Wageningen University, Wageningen, the Netherlands.
- Sabelis MW, van Baalen M, Pels B, et al (2002) Evolution of exploitation and defence in tritrophic interactions. In Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds.). *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*. Cambridge Univ. Press, Cambridge, pp. 297-326.
- Stevens VM, Trochet A, Blanchet S, et al (2013) Dispersal syndromes and the use of life-histories to predict dispersal. *Evol Appl* 6:630–642.
- Stevens VM, Whitmee S, Le Galliard J-F, et al (2014) A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. *Ecol Lett* 17:1039–1052.
- Taylor AD (1990) Metapopulations, Dispersal, and Predator-Prey Dynamics: An Overview. *Ecology* 71:429–433.
- Tsolakis H, Tixier MS, Kreiter S, Ragusa S (2012) The concept of genus within the family Phytoseiidae (Acari: Parasitiformes): historical review and phylogenetic analyses of the genus *Neoseiulus* Hughes. *Zool J Linn Soc* 165:253–273.
- van Baalen M, Sabelis MW (1995) The Milker-Killer Dilemma in Spatially Structured Predator-Prey Interactions. *Oikos* 74:391–400.
- Walsh PS, Metzger DA, Higuchi R (1991) Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *Biotechniques* 10:506–513.
- Weisser WW, McCoy KD, Boulinier T (2001) Parasitism and predation as causes of dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds), *Dispersal*. Oxford Univ. Press, New York, pp. 168-188.
- Wiens JA (2001) The landscape context of dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds), *Dispersal*. Oxford Univ. Press, New York, pp. 96-109.



## Supplementary material

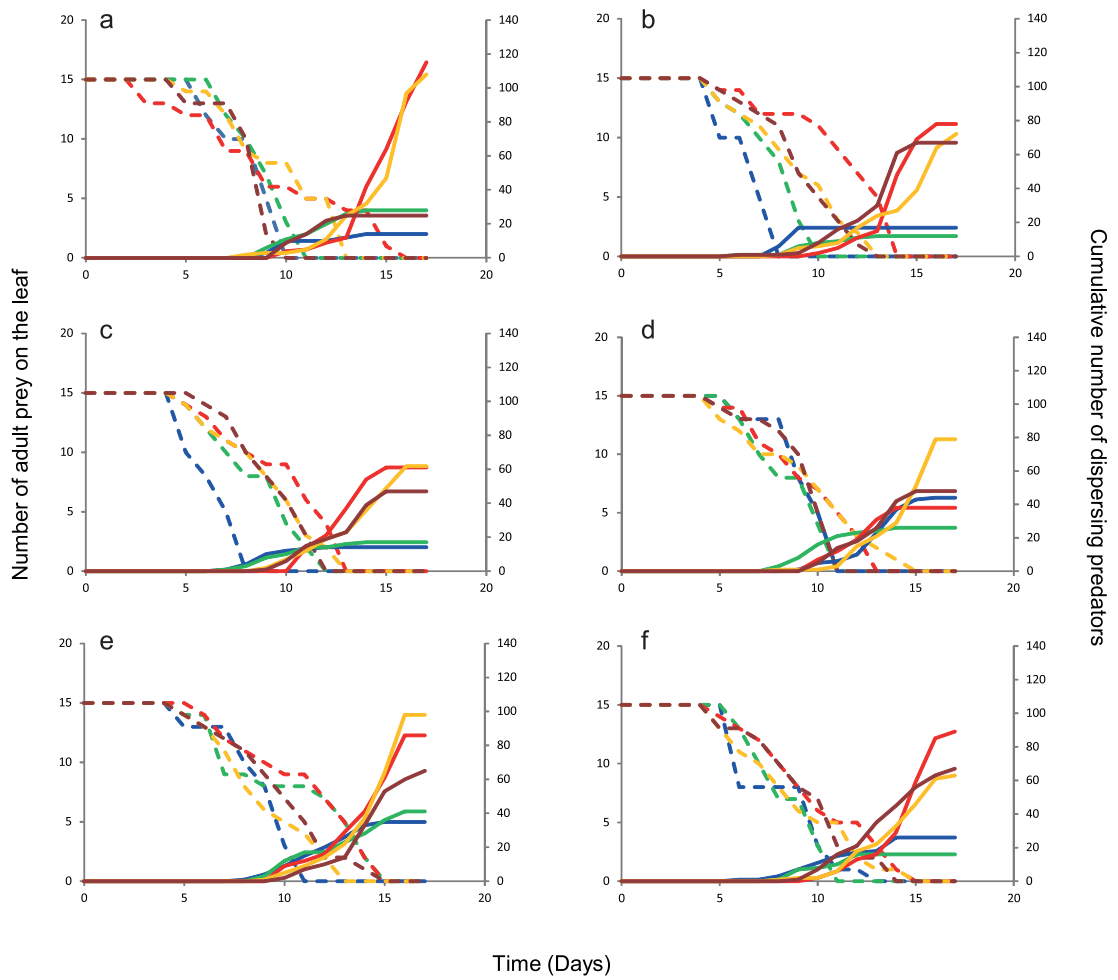
**TABLE S2.1** — Timetable of when each strain of *Phytoseiulus persimilis* was collected, cultured and tested

Origin	Strain	Date of collection	Date of culture	Replicate	Date of testing
Turkey	Samandağ	17-Jul-2013	22-Jul-2013	a	25-Nov-2013
				b	23-Dec-2013
				c	13-Jan-2014
				d	10-Feb-2014
				e	3-Mar-2014
	Koyunoğlu	16-Jul-2013	22-Jul-2013	a	25-Nov-2013
				b	23-Dec-2013
				c	13-Jan-2014
				d	10-Feb-2014
				e	3-Mar-2014
	Kuşalanı	16-Jul-2013	22-Jul-2013	a	25-Nov-2013
				b	23-Dec-2013
				c	13-Jan-2014
				d	10-Feb-2014
				e	3-Mar-2014
	Karaçay	17-Jul-2013	22-Jul-2013	a	25-Nov-2013
				b	23-Dec-2013
				c	13-Jan-2014
				d	10-Feb-2014
				e	3-Mar-2014
	Uzunbağ	16-Jul-2013	22-Jul-2013	a	25-Nov-2013
				b	23-Dec-2013
				c	13-Jan-2014
				d	10-Feb-2014
				e	3-Mar-2014
Kocahasanlı	19-Jul-2013	22-Jul-2013	a	25-Nov-2013	
			b	23-Dec-2013	
			c	13-Jan-2014	
			d	10-Feb-2014	
			e	3-Mar-2014	
Sicily	Castelvetrano	4-Jun-2014	8-Jun-2014	a	25-Nov-2013
				b	23-Dec-2013
				c	13-Jan-2014
				d	10-Feb-2014
				e	3-Mar-2014
	Trabia	5-Jun-2014	8-Jun-2014	a	22-Sep-2014
				b	4-Nov-2014
				c	1-Dec-2014
				d	26-Jan-2015
				e	17-Feb-2015
	Alcamo	4-Jun-2014	8-Jun-2014	a	22-Sep-2014
				b	4-Nov-2014
				c	1-Dec-2014
				d	26-Jan-2015
				e	17-Feb-2015

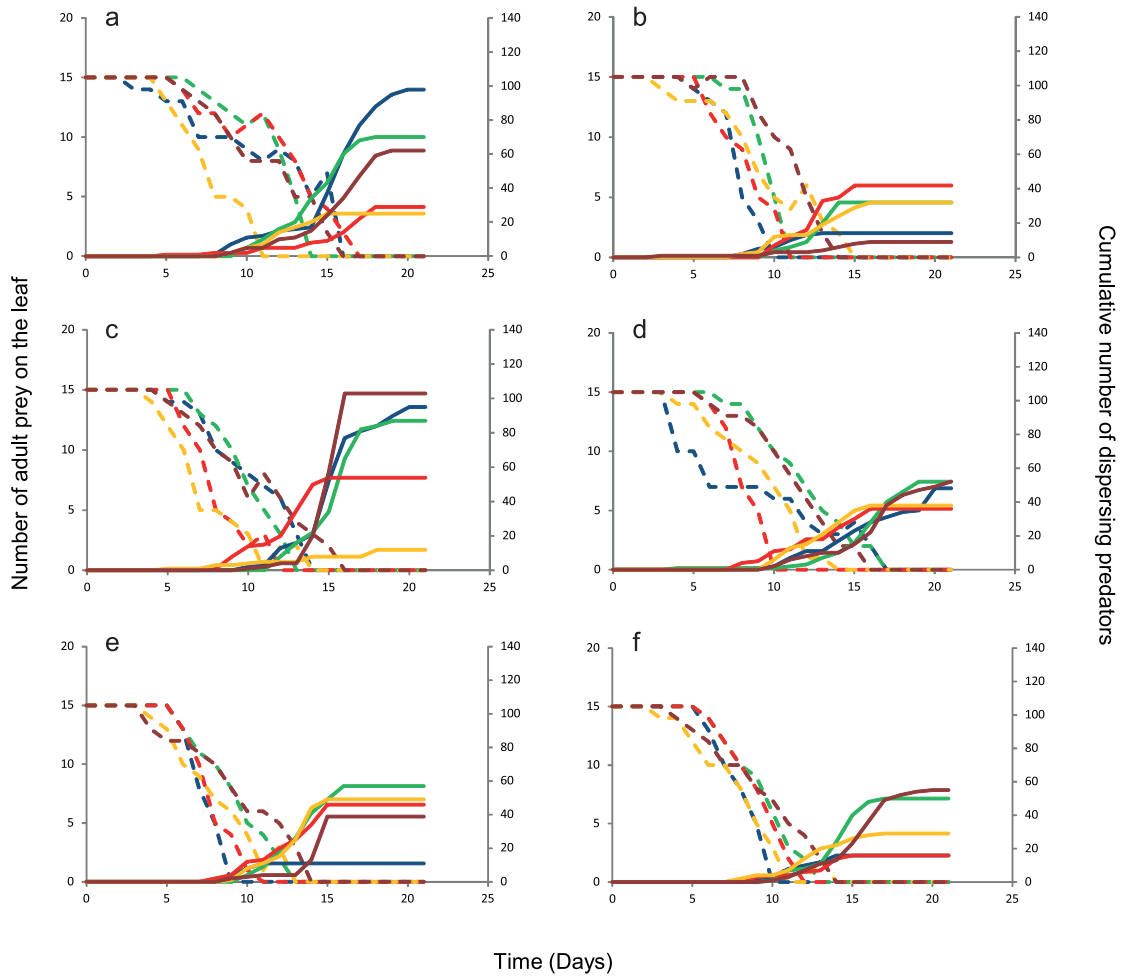
Origin	Strain	Date of collection	Date of culture	Replicate	Date of testing
	Lascari	5-Jun-2014	8-Jun-2014	a	22-Sep-2014
				b	4-Nov-2014
				c	1-Dec-2014
				d	26-Jan-2015
				e	17-Feb-2015
	Palermo	4-Jun-2014	8-Jun-2014	a	22-Sep-2014
				b	4-Nov-2014
				c	1-Dec-2014
				d	26-Jan-2015
				e	17-Feb-2015
Koppert	Koppert	1-Jan-1994	4-Sep-2014	a	22-Sep-2014
				b	4-Nov-2014
				c	1-Dec-2014
				d	26-Jan-2015
				e	17-Feb-2015

TABLE S2.2 — Average population growth rate ( $\gamma$ ) per strain of *Phytoseiulus persimilis*

Origin	Strain	$\gamma \pm SE$	Origin	Strain	$\gamma \pm SE$
Turkey	Samandağ	0.41 $\pm$ 0.02	Sicily	Castelvetrano	0.36 $\pm$ 0.02
	Koyunoğlu	0.39 $\pm$ 0.04		Trabia	0.38 $\pm$ 0.05
	Kuşalanı	0.38 $\pm$ 0.03		Alcamo	0.40 $\pm$ 0.03
	Karaçay	0.39 $\pm$ 0.03		Lascari	0.37 $\pm$ 0.03
	Uzunbağ	0.41 $\pm$ 0.03		Palermo	0.41 $\pm$ 0.03
	Kocahasanlı	0.39 $\pm$ 0.03		Koppert	Koppert



**FIGURE S2.1** — Population dynamics of adult prey (*Tetranychus urticae*) on the leaf (dashed lines, left-hand vertical axis) and cumulative number of dispersing predators (*Phytoseiulus persimilis*) (solid lines, right-hand vertical axis). Different color corresponds to different replicate. Blue: replicate 1, Green: replicate 2, Red: replicate 3, Orange: replicate 4 and Purple: replicate 5. a: Samandağ, b: Koyunoğlu, c: Kuşalanı, d: Karaçay, e: Uzunbağ, f: Kocahasanlı.



**FIGURE S2.2** — Population dynamics of adult prey (*Tetranychus urticae*) on the leaf (dashed lines, left-hand vertical axis) and cumulative number of dispersing predators (*Phytoseiulus persimilis*) (solid lines, right-hand vertical axis). Different color corresponds to different replicate. Blue: replicate 1, Green: replicate 2, Red: replicate 3, Orange: replicate 4 and Purple: replicate 5. a: Castelvetro, b: Trabia, c: Alcamo, d: Lascari, e: Palermo, f: Koppert.