

Response of a complex foraging phenotype to artificial selection on its component traits

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Received: 2 February 2009 / Accepted: 14 July 2009
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Abstract In nature, where predators must often track dynamic and dispersed prey populations, predator consumption rate, conversion efficiency, dispersal, and prey finding are likely to be important links between foraging and predator–prey population dynamics. Small differences in predator foraging caused by variation in any of the abovementioned traits might lead to significant differences in predator success as well as population dynamics. We used artificial selection to create lines of the predatory mite, *Phytoseiulus persimilis* in order to determine the potential for or constraints on the evolution of predator foraging behaviors. All four foraging traits demonstrated considerable phenotypic variation. They also exhibited significant realized heritabilities after artificial selection, except that prey finding did not respond to downward selection. Lines that responded to selection did so rapidly, and high-consumption, high-conversion efficiency, and high- and low-dispersal were stable for at least four generations after artificial selection was relaxed. There were some indirect responses to selection among the foraging traits. For example, there was positive correlation between consumption and dispersal. However, none of the

Electronic supplementary material The online version of this article (doi:[10.1007/s10682-009-9318-0](https://doi.org/10.1007/s10682-009-9318-0)) contains supplementary material, which is available to authorized users.

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correlated responses were of the magnitude of the direct responses we measured on the same trait. We also observed some correlations between foraging traits and life-history traits such as low-consumption and development time (negative), high-consumption and fecundity (positive), and high-conversion efficiency and fecundity (positive), but these were more likely to represent non-genetic constraints. Intrinsic rates of increase in low-consumption and low-conversion efficiency lines were lower than in their respective high lines and the unselected control, whereas rates of increase in dispersal and olfactory response lines did not differ from the unselected control. Thus, traits that make up foraging share partially overlapping genetic architectures with highly heritable phenotypic components, suggesting that each foraging trait will be able to respond rapidly to changes in the density and distribution of resources.

Keywords Heritability · Life-history traits · Foraging behavior · Predatory mite · Twospotted spider mite · Predator–prey interaction

Introduction

How animals forage for food is a core issue in ecology. This process forms the basis of trophic interactions and plays a fundamental role in shaping population dynamics, food webs, and communities. Foraging is the expression of a complex phenotype that is composed of numerous behavioral and physiological components, including importantly those that affect movement and consumption. The manner in which sets of phenotypic traits respond to selection has and continues to be a central issue of evolutionary theory (Lande and Arnold 1983; Roff 1992; Stearns 1992). Ecological factors such as the density, distribution and variability of resources and the risks associated with searching for food may affect the success associated with each of these components differently (Stephens and Krebs 1986; Ives et al. 1993). Furthermore, ecological factors not directly related to foraging, such as variation in life-history traits, may also affect foraging success (Roitberg et al. 1992).

Despite a continuing interest in the effect of the resource environment on foraging success (e.g., Pimentel et al. 1963; Lawton 1983; Kareiva and Sahakian 1990), we know relatively little about the genetic basis of ecologically-relevant foraging traits that might drive evolution of predator–prey ecological interactions. For any complex phenotype to evolve in response to ecological conditions it is essential that the phenotypic variation be controlled in part by heritable genetic variation. At a genetic level there may be tremendous variation in foraging among individuals of a species owing to the interaction of many genes (Sokolowski 2001). However, genetic correlations with other traits may alter the rate and direction of the response to selection (Arnold 1986). In order to generate testable hypotheses about the evolution of foraging behaviors we must first determine to what extent these behaviors are heritable. This, plus knowledge of the correlations among foraging components and other traits, provides a basis to more accurately predict population responses to selection in fluctuating environments.

We have started to address the evolution of foraging by conducting a set of artificial selection experiments focusing on several specific, phenotypically variable predator foraging traits that potentially affect both predator fitness and predator–prey population dynamics in spatially and temporally variable environments. Specifically, we used artificial selection to create lines of a predatory mite that differed by a single trait in order to

determine the potential for or constraints on the evolution of predator-foraging traits. Artificial selection experiments provide a powerful tool to estimate genetic variation and gain insight into the genetic control of traits by investigating the symmetry, limits, and stability of the responses to selection (Falconer and Mackay 1996). Such experiments can also be used to estimate the strength and sign of correlations that underlie multiple phenotypic components by quantifying the correlated response to selection. We used this approach to examine genetic variation in, and correlations among, predator foraging traits in a tightly linked predator–prey system consisting of the predatory phytoseiid mite, *Phytoseiulus persimilis* Athias–Henriot and its prey, the herbivorous twospotted spider mite, *Tetranychus urticae* Koch.

Phytoseiulus persimilis and *T. urticae* populations exist in clusters or patches on plants or groups of plants. The local (i.e., within patch) interaction between *P. persimilis* and *T. urticae* is often ephemeral because, when *P. persimilis* invade a spider mite-infested plant, the predators quickly eliminate the local spider mite population (Chant 1961; Takafuji et al. 1983; Sabelis and van der Meer 1986). However, while the local interaction is generally unstable, the predator–prey interaction may persist on a regional scale as a result of repeated dispersal from and colonization of new patches by both prey and predators (Diekmann et al. 1988; Nachman 1988, 1991; Sabelis et al. 1991; Janssen and Sabelis 1992; McCauley et al. 2000; Ellner et al. 2001; Sabelis et al. 2005). Two traits, the rate of prey consumption by predators and the efficiency with which predators convert prey eaten into new predators, reflect the basic link between predator foraging and population dynamics in homogeneous environments, as would be the case within a patch (Sabelis 1985; Sabelis et al. 1999). However, in heterogeneous environments, traits that affect colonization success, such as predator dispersal rates from existing prey patches and the ability of dispersing predators to find new prey patches, affect both individual foraging success and regional predator–prey dynamics (Hassell 1978; Berryman and Gutierrez 1999; Ellner et al. 2001; Sabelis et al. 2005).

The first objective of this study was to quantify the genetic contribution to phenotypic variation in consumption rate, reproductive conversion efficiency, dispersal and prey finding in *P. persimilis*. Previous work on variation among inbred lines has shown additive genetic variation in consumption, oviposition, dispersal and prey finding/aggregation in *P. persimilis* (Pels and Sabelis 1999; Jia et al. 2002) and the related predatory mite *Neoseiulus womersleyi* (Maeda 2006). However, inbred lines provide only a limited sampling of the total genetic variation; if the traits of interest are linked to fitness this may result in skewed estimates of genetic variation. In addition, we were particularly interested in the rate of and limits to the selection response, which cannot be deduced from studies that quantify genetic variation among inbred lines. Selection limits may be imposed on a population either because of genetic constraints caused by correlated traits or as a result of the fixation of alleles affecting the trait. Our second objective was to investigate the cause of these limits to selection by quantifying the correlated responses in consumption, conversion efficiency, dispersal and olfactory response among all lines subjected to selection. Additionally, we measured correlated responses of life history traits, including time to emerge from egg, hatching percent, development time (time from nymph to adult ecdysis), survivorship from egg to adult and fecundity. To our knowledge this is the first experimental study that examines the genetic basis of a set of ecologically-relevant foraging traits that are likely to be critical for predator performance and predator–prey dynamics in heterogeneous landscapes.

Materials and methods

Predators

The predatory mite *P. persimilis* (Acari: Mesostigmata: Phytoseiidae) is unusual in that it is an extreme feeding specialist, requiring spider mites for its development and reproduction. The origin of the predator is not clear, but it is thought to be of Mediterranean or South American origin (Dosse 1958). However, since the 1960's it has been shipped to and established in many parts of the world as a biological control agent for spider mites, particularly the twospotted spider mite *T. urticae* (Acari: Prostigmata: Tetranychidae) (Kennett and Caltagirone 1968). Phytoseiid mites reproduce by pseudoarrhenotoky, which is characterized by obligate fertilization of all eggs followed by a loss and/or heterochromatization of the paternal chromosomes in embryos that develop into males, resulting in a haploid condition of the males (Hoy 1979; Schulten 1985; Perrot-Minnot et al. 2000). Under normal conditions, the sex ratio is female-biased, usually close to 0.83 (Helle and Sabelis 1985) and each female produces 3–4 eggs per day, which results in 60 eggs in her lifetime (McMurtry and Rodriguez 1987). *Phytoseiulus persimilis* has five developmental stages: egg, non-feeding larva, protonymph, deutonymph and adult (Sabelis 1981). Development time (egg to adult) at 25°C is approximately 3 days, generation time (egg to egg) is 5 days, and average adult lifespan is 25 days (Takafuji and Chant 1976).

Selected lines were initiated from a source population of 600–700 adult female *P. persimilis* that was purchased from Koppert Biological Systems, Inc. (Romulus, Michigan), a commercial supplier of beneficial arthropods. The source population exhibited wide phenotypic variation in all four traits of interest (Supplementary Fig. 1). Upon receipt, *P. persimilis* were reared on their natural prey, twospotted spider mites, in the laboratory for one generation at $24 \pm 1^\circ\text{C}$, 60–70% relative humidity, 16:8 h (L:D) photoperiod prior to initiation of selection regimes to allow the population to become acclimatized to laboratory conditions. *Tetranychus urticae* (prey) were maintained on lima beans (*Phaseolus lunatus* cv. 'Sieva') under the same temperature and photoperiodic regime. Selection lines were maintained in 1.89 l mason jars with the metal lids removed and replaced with fine mesh screen to allow air exchange. Prey-infested bean plants were added to the jars every other day. Every week the bottom layers, consisting of dry leaves with few spider mites or predators, were discarded. Seven to ten-day old adult female predators were used for all experiments.

Artificial selection

We selected for *P. persimilis* with extreme levels (relative to an unselected control population) of the four described foraging traits: consumption rate, conversion efficiency, dispersal response to prey density, and olfactory attraction to *T. urticae*-induced plant volatiles. To determine whether observed phenotypic changes that might occur in response to selection are the result of selection rather than effects of random genetic drift, selection experiments usually include contemporaneously replicated lines within each selection treatment (Falconer and Mackay 1996; Morgan et al. 2003). However, we were faced with logistical constraints that prevented us from maintaining contemporaneous replicate lines when performing selection on foraging behavioral phenotypes in *P. persimilis*; these constraints were primarily caused by the large amount of time required to set up and conduct the assays for each trait coupled with the short generation time of the mites. Rather than eliminating replication from our selection experiment, we chose to repeat selection on

the same source population at different times. We started the first round of selection by imposing mass individual selection each generation. But after two generations the numbers became too low and we switched to family selection to allow numbers to increase (See section “[Selection regime I](#)” below). In the second round of selection we solved this problem using a more typical selection regime in which we alternated selection and no selection; that is, we imposed selection on the first generation, allowed the second generation to mate without selection, imposed selection on the third, generation, and so on (See section “[Selection regime II](#)” below). This allowed us to use a consistent selection regime and still obtain population sizes large enough to phenotype and use for artificial selection.

Selection regime I

Bidirectional selection was initiated using mass individual selection (Falconer and Mackay 1996). Consumption and conversion efficiency lines were initiated by phenotyping 200–350 individuals from a randomly mating source population, whereas the dispersal and olfactory response lines were initiated from 170 to 200 individuals. From these initial populations, one line was selected for increased trait values and one line for decreased trait values using a 20% criterion; the same percentage of individuals was selected each time selection was imposed to form the subsequent generations (Supplementary Table 1). At the same time the selected lines were started, an unselected control population was started with 100 adult females from the source population. The control population was maintained with 50–100 adult females throughout the experiment. In order to keep generations separated and test only even-aged individuals, adults from one generation were only allowed to oviposit for 3 days and then removed. As a result of these criteria, we saw dramatic reductions in the number of offspring available for the following round of selection after two generations of individual mass selection for consumption and conversion efficiency and three generations of selection for dispersal and olfactory response. Therefore, to increase our sample size we modified the selection protocol by establishing isofemale lines and imposing family selection for one generation.

We started family selection by creating 10–20 families with the females selected from the 20% tail of the previous generation. For family selection a whole family represents the breeders for the next generation as a unit according to its mean phenotypic value (Lynch 1980; Falconer and Mackay 1996). We assayed the adult offspring of these isofemale families and selected 3–4 families to continue each selection line (approximately 25% selection criterion). From these selected families we took 8–10 adult females and pooled them to form the next generation. Their offspring were allowed to breed without selection to increase the population size of each line. Individual selection was resumed for the next generation and continued until there was no longer any change in the phenotypic trait mean. We acknowledge that this bottleneck imposed by the dip in population size likely resulted in a few generations where genetic drift was quite pronounced. However, we believe that the consistency between our first and second (see below) replicates of selection insures that the observed phenotypic responses are the result of changes in the allele frequencies caused by artificial selection and not as a result of random fluctuations caused by drift.

Artificial selection on consumption, conversion efficiency, dispersal or olfaction might be opposed by the action of natural selection acting on these traits, or some other correlated traits, in the direction opposite of the artificial selection. If this were the case, we would expect the phenotypic response observed in the selection lines would be lost when

selection was relaxed. To test this possibility, selection was no longer imposed (i.e., relaxed) after the generation in which the selection response was 0 (i.e., selection had plateaued). This occurred after generation six for all traits except for consumption, in which selection was relaxed after generation seven. After selection was relaxed these lines were maintained by collecting 50–60 offspring from each line in the same manner described in the selection experiment. Levels of consumption, conversion efficiency, dispersal and olfaction were measured after 10–12 generations of relaxed selection and within line random mating at which time we tested 40–50 adult female *P. persimilis* from each selection line.

Selection regime II

For those traits in which selection appeared to be stable after selection was relaxed (high-consumption, high-conversion efficiency and high-dispersal response) we repeated selection from the source population. The selection lines in the second replicate were initiated from a different cohort purchased from Koppert. Predator conditions and age of predators were identical to those in the first round of the selection experiment, as were the range and frequency distribution of the traits. Selection was initiated by phenotyping 80–100 adult female predators from the source population for each trait. Selection was imposed as before by utilizing the breeding individuals that made up the 20% tail of the population distribution (Supplementary Table 1). Individual mass selection was used for each selection event. However, because of the difficulties encountered in the maintenance of sufficient population sizes during the first replicate, in the second replicate we selected every other generation until no further change in the trait was observed. An unselected control was maintained as in selection regime I. We did not quantify the stability of the response after selection plateaued under the second selection regime.

Phenotypic bioassays

Consumption and conversion efficiency

Phytoseiulus persimilis nymphs and adults feed on all stages of their tetranychid prey but preferentially consume prey eggs (Sabelis 1981, 1986, 1990); when prey are abundant, adults will consume an average of 24 prey eggs per day (Sabelis 1981). Predators normally produce 4 offspring per day, or one predator egg produced for every 6 prey eggs consumed (Sabelis 1981, 1986, 1990; Janssen and Sabelis 1992; Sabelis and Janssen 1993). Consumption and conversion efficiency were measured in a bioassay developed by Jia et al. (2002). *P. persimilis* were placed in a vial 2.5-cm diameter \times 5.5-cm height along with a 2.2-cm diameter bean leaf disk that had 40–50 one-day old *T. urticae* eggs. The vial was sealed with Parafilm[®] and maintained in an environmental chamber at $24 \pm 1^\circ\text{C}$, 60–70% relative humidity, and 16:8 h L:D photoperiod for 24 h, after which the number of prey eggs left on the disk was counted. In addition, predator eggs generated within the 24-h period were also counted. Consumption rate was defined as the number of prey eggs consumed by a predatory mite within 24 h and conversion efficiency was the ratio of the number of prey eggs consumed to the number of predator eggs laid in that time. An unselected control was maintained during the experiment but was not tested for consumption and conversion efficiency until after the traits plateaued.

Dispersal response

Predatory mites usually disperse from occupied patches when prey density approaches zero (Takafuji 1977; Sabelis 1981; Bernstein 1984; Zhang and Sanderson 1993; Zemek and Nachman 1998). However, this response is variable and some individuals disperse even in the presence of abundant prey (Nachappa et al. 2006a). Dispersal of *P. persimilis*, defined as the time to leave a prey patch, was measured in a petri dish bioassay modified from Maeda and Takabayashi (2001) and Nachappa et al. (2006a). A 2.2-cm diameter leaf disk with *T. urticae* eggs was placed on water-saturated cotton wool in 90-cm diameter plastic petri dish. Ten *T. urticae* (prey) adult females were introduced on the leaf disk and allowed to oviposit for 24 h; eggs were removed to achieve the appropriate density on the leaf disk or source (see following paragraph for details). Five *P. persimilis* adult females were then introduced onto each leaf disk and allowed a 30 min acclimatization period, after which we connected a 30 × 5 mm Parafilm® bridge to the disk. Predators that walked onto and out along the bridge were counted as dispersed. Predators were observed continuously and were removed as soon as they came to or passed the midpoint of the bridge. The time taken to disperse was then recorded.

Previous research has shown that time to disperse by *P. persimilis* is significantly affected by prey density (40 vs. 5 prey eggs) (Nachappa et al. 2006a). Thus, in this study the high-dispersal line represents those individuals that dispersed from the leaf disk in the presence of 40 eggs (an abundant resource), while the low-dispersal line is comprised of individuals that remained on the leaf disk in the presence of only 5 eggs. Because the high- and low-dispersal lines were selected under different environmental test conditions (40 vs. 5 prey eggs) it was inappropriate to directly compare the high and low selection lines. Thus, the high and low selection lines were each compared to an unselected control each generation rather than to each other.

Olfactory response

When spider mites feed on bean plants, the plants produce a unique blend of volatile compounds to which *P. persimilis* respond more strongly than they do to uninfested bean plants (Sabelis and van de Baan 1983; Sabelis et al. 1984; Dicke et al. 1990a, b; Takabayashi et al. 1991). The presence of prey-induced plant volatiles increases the ability of *P. persimilis* to find its prey in heterogeneous habitats (Janssen 1999) either by attraction to or reduced leaving from prey patches. We measured the attraction/arrestment response of *P. persimilis* to *T. urticae*-infested leaves using a 40-cm diameter circular arena as in Jia et al. (2002) and Nachappa et al. (2006b). Selection for high- and low-response lines was conducted using two different levels of volatiles; we used a low level of volatiles to select for the high-olfaction line and high levels of volatiles to select for the low-olfaction line. To achieve high- or low-volatile production we manipulated prey density on bean plants for different durations of time (for details see Nachappa et al. 2006b). Leaf disks (2.2 cm diameter) cut from the manipulated plants then served as the source of the two different volatiles levels for selection. Test conditions were similar to those followed in Nachappa et al. (2006b).

Phenotyping was performed in two arenas that were set up side-by-side with a vertical cardboard divider (60 cm ht × 55 cm w) between them to reduce air movement and possible drift of volatiles (Jia et al. 2002). In the center of one arena we placed a leaf disk from a *T. urticae*-infested plant; in the other we placed a leaf disk from an uninfested plant as a control. Comparisons between the test disks (infested plant) and control disks (clean plant) provided a control to examine if the observed response differed from that expected under random (non-attracted) movement. Thus, this experimental assay allowed us to be

sure that any change in behavior following selection was the result of a change in olfactory response and not a change in overall activity levels. For each trial, 10–12 adult female predatory mites were starved for 2 h and then released at the edge of the arena. We recorded the number of predators that found the central leaf disk (source of volatiles) in the arena in the first 10 min. The high response line consisted of individuals that found the central leaf disk in the presence of low volatile level in the vicinity (arena). The low response line consisted of individuals that did not find the leaf disk despite a high level of volatiles in the arena. However, the low olfactory response individuals were actively moving around the arena and not stationary; this confirmed that they were not just diseased or otherwise impaired. The high and low response lines were selected under different environmental conditions; hence we did not directly compare them but each was compared to an unselected control every generation.

Indirect responses to selection

Foraging traits

We examined correlated responses to selection among consumption, conversion efficiency, dispersal and olfactory response for all lines subjected to the first selection regime after selection plateaued. The cohorts that were used to assay the correlated responses to selection were initiated by randomly choosing 10–15 adult female predators from each selection line. Each foraging phenotype was then measured using previously described bioassays (see section “[Phenotypic bioassays](#)”).

Life-history traits

We developed a life table to estimate life-history parameters and genetic correlations between life history traits and selected traits in each selection line created by the first selection regime. A life table was also developed for the unselected control population maintained for selection regime I. To estimate the life table of each line it is essential to have a cohort of age-synchronized individuals. Thus, we used ten to fifteen adult female predators to produce a cohort of offspring from each selection line. These females were placed on whole leaves set abaxial side up on water-saturated cotton wool in 90-cm diameter plastic petri dish. The adult female predators were allowed to oviposit for 24 h. The cohort upon which the life-history traits were measured was initiated by collecting 30–41-day old predator eggs from each line and placing them individually on a 2.2 cm diameter leaf disk which was inserted into small glass vial. The vial was sealed with Parafilm[®] and maintained in an environmental chamber at $24 \pm 1^\circ\text{C}$, 60–70% relative humidity, and 16:8 h L:D photoperiod. The vials were inspected and prey eggs were provided as food daily. Once nymphs reached adulthood, adult females were placed as a group in a single vial for 4–8 h under the environmental conditions mentioned above to allow mating within the cohort. Ten mated adult females were then placed individually in vials under similar environmental conditions as described above. The vials were checked daily and prey eggs were provided as food until <50% of the population were alive. The life-history traits measured were hatching time (time to emerge from egg), hatching percent, development time (time from nymph to adult ecdysis), survivorship from egg to adult of individual adult females.

Based on the complete life table, we calculated the intrinsic rate of natural increase, r_m for each selection line assayed in the test population. The intrinsic rate of increase can be computed as a solution to:

$$1 = \sum l_x m_x e^{-r_m x}$$

where l_x is the fraction of females alive at age x , and m_x is the average number of female offspring produced by each female at age x (Birch 1948; Carey 1993). This equation was iterated for r_m until a value of one was obtained. The jackknife method of re-sampling is commonly used for estimating variance for population-growth statistics (Meyer et al. 1986). Estimates of standard errors for these demographic growth parameters were generated by jackknife analysis of life-table data (Shao and Tu 1995; Meyer et al. 1986).

Statistical analysis

All analyses were conducted using the statistical program SAS v 9.1 (SAS Institute 2002). To measure the response to selection a one-way Analysis of Variance (ANOVA) was performed to identify direct responses to selection between the high- and low-lines for consumption and conversion efficiency under selection regime I. Similarly, a one-way ANOVA was used to determine the direct responses to selection for dispersal and olfactory response by comparing the selection lines (i.e., high or low) with the unselected control lines rather than with each other, because the high- and low-lines for each trait were selected under different environmental conditions. These models test for differences in the mean phenotypic values each generation between selection lines (high vs. low) or between the selected line and the unselected control (e.g., high vs. control).

To evaluate the stability of the selection lines after artificial selection was relaxed, we compared the mean phenotypic value of cohorts sampled from the high and low lines, after these lines had been maintained without imposition of selection for 10–12 generations, with the unselected control using a one-way ANOVA. The presence of significant differences between the high (or low) line and the unselected control line after selection was relaxed is evidence that the selection response was stable. For the dispersal and olfactory response lines, relaxation effects were examined using a one-way ANOVA which compared the trait values after selection was relaxed relative to the environment-specific unselected control line for dispersal and olfactory response.

A univariate ANOVA analysis was performed between selection lines of regime I and II for each of the phenotypes common to the two regimes. A non-significant difference in these analyses implies a consistent response to selection regardless of selection regime. Although this is an atypical method of evaluating the consistency of the selection response, in that it does not compare replicated selection lines to replicated unselected control lines (Morgan et al. 2003), the inferences gained from this analysis of the consistency of the selection response are identical to more typical analyses involving comparison to replicated control lines.

We calculated the realized heritability (h^2) for each selection line from both selection regimes by regressing the cumulative selection differential (s) on the cumulative selection response (R). The selection response and the selection differential were calculated for each generation in which selection was applied (in generations where selection was not imposed $s = 0$) (Falconer and Mackay 1996). The selection differential (s) was calculated each generation as the difference between the phenotypic mean of selected parental population relative to the mean of the entire population. The response to selection (R) was calculated as the difference between the phenotypic mean of the progeny and the phenotypic mean of the previous generation (Falconer and Mackay 1996). The realized heritabilities (h^2) and associated standard errors were calculated in PROC GLM by regressing the $\sum s$ on $\sum R$. The slope

of this relationship represents the line-specific estimate of the heritability (Falconer and Mackay 1996).

The following analyses were performed to measure correlated responses to selection under selection regime I. A one-way ANOVA (PROC GLM) was used to measure the correlated responses in consumption rate and conversion efficiency between the high and low selection lines for each of the other foraging traits and unselected control population. Correlated responses to selection for dispersal were calculated using a two-way ANOVA with effects of selection lines (high and low), unselected control and prey density in the model. The correlated responses to selection on olfactory attraction were also calculated using a two-way ANOVA with effects of selection line, unselected control and volatile level in the model. Two-way ANOVAs were used to assay the correlated responses to selection on dispersal and olfactory response because these traits are environmentally-dependent. That is a correlated response to selection may only be present in one of the two environments in which each of these phenotypes was measured. Thus the terms of primary interest in these two-way analyses are the line term which would suggest a general correlated response to selection that is consistent across environments and the interaction between line and environment (i.e., prey density or volatile level) which would suggest an environmentally dependent correlated response to selection (i.e., genotype by environment interaction). A one-way ANOVA was used to test for correlated responses to selection in the different life-history traits (i.e., hatching time, hatching percent, development time, daily adult survival and fecundity). Mean jackknife estimates of intrinsic rate of increase (r_m) were compared between high and low lines and unselected control for each foraging trait using a one-way ANOVA.

Results

Direct response to selection: heritability and stability

Consumption

Selection regime I significantly affected mean prey egg consumption in the high and low lines in generation 1 ($F_{1,155} = 78.25$, $P < 0.0001$; Fig. 1). The high- and low-consumption lines were highly differentiated at the end of the 7-generation period ($F_{1,24} = 801.22$,

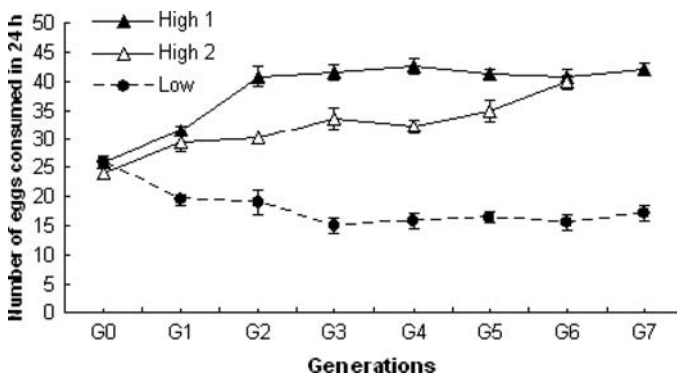


Fig. 1 Mean (\pm SE) prey consumption (24 h) per generation for *P. persimilis* subjected to different selection regimes

$P < 0.0001$; Fig. 1). Prey consumption rate responded rapidly to selection with an asymmetrical response; it was more pronounced in the high line than in the low line (Fig. 1). There were significant differences among the high- and low-consumption lines after selection was relaxed relative to the unselected control line (measured in selection regime I only, $F_{2,120} = 131.99$, $P < 0.0001$). The high-consumption line remained at high levels despite relaxation of selection, but in the low line the prey consumption rate increased significantly when selection was discontinued so that it was no longer different than the unselected control (mean prey consumption rate \pm SE, high line: 40.76 ± 0.63 ; low line: 28.90 ± 0.58 ; unselected control: 27.16 ± 0.68).

To confirm that the lines were in fact responding to selection and not simply diverging because of random genetic drift, we performed a second selection experiment but only on those phenotype that showed stability after the first experiment. The prey consumption rate was not significantly different between the high lines from the two selection regimes at the end of the experiment ($F_{1,55} = 1.13$, $P = 0.29$; Fig. 1, mean consumption \pm SE, high line selection regime I: 42.00 ± 1.71 ; high line selection regime II: 39.91 ± 0.98). The selection response was more rapid in selection regime I than selection regime II because in the former selection was imposed every generation (except generation 3 and 4) whereas selection was imposed every other generation in selection regime II. Realized heritability estimates of the high and low lines were significant and greater than zero (Table 1). Realized heritabilities for high-consumption lines were comparable between the two selection regimes (Table 1; Supplementary Fig. 2).

Conversion efficiency

There was significant differentiation between the high- and low-conversion lines after one generation of selection ($F_{1,145} = 144.48$, $P < 0.0001$; Fig 2). This difference was maintained throughout the rest of the selection experiment. After selection was relaxed, the high-conversion efficiency line remained significantly higher than the low line and the control whereas the low-conversion efficiency line was comparable to the control population (measured in selection regime I only, $F_{2,111} = 131.99$, $P = 0.008$; mean conversion efficiency \pm SE, high line: 0.18 ± 0.013 ; low line: 0.11 ± 0.014 ; control: 0.13 ± 0.014). The second replicate of the high-conversion efficiency line was not significantly different

Table 1 Realized heritability (h^2) of foraging traits in *P. persimilis*

Trait	Line	Heritability \pm SE	<i>P</i>
Consumption	High 1	0.48 ± 0.11	0.01
	High 2	0.42 ± 0.003	<0.0001
	Low	0.26 ± 0.13	0.05
Conversion efficiency	High 1	0.44 ± 0.16	0.05
	High 2	0.56 ± 0.15	0.02
	Low	0.20 ± 0.02	0.002
Dispersal response	High 1	0.29 ± 0.02	<0.0001
	High 2	0.28 ± 0.009	<0.0001
	Low	0.64 ± 0.11	0.005
Olfactory response	High	0.08 ± 0.02	0.023
	Low	0.01 ± 0.04	0.83

Significant *P*-values indicates that the heritabilities are different than 0

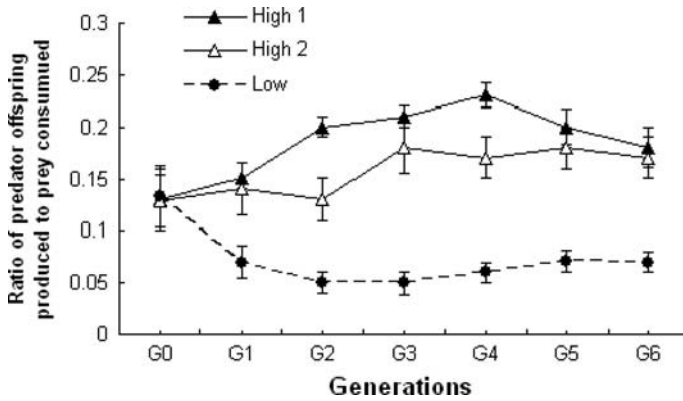


Fig. 2 Mean (\pm SE) conversion efficiency (24 h) per generation for *P. persimilis* subjected to different selection regimes

from selection replicate I at the end of the experiment ($F_{1,78} = 0.07$, $P = 0.79$; Fig. 2, mean conversion efficiency \pm SE, high line selection regime I: 0.17 ± 0.007 , high line selection regime II: 0.17 ± 0.01). Realized heritability estimates from the high- and low-conversion lines were significantly greater than zero (Table 1). Realized heritabilities for the high-conversion efficiency lines were comparable between the two selection regimes (Table 1; Supplementary Fig. 3).

Dispersal response

High- and low-dispersal lines were selected under different environmental test conditions so each was compared to an unselected control. After the first generation of selection, the high-dispersal line was differentiated from the unselected control ($F_{1,154} = 52.29$, $P < 0.0001$, Fig. 3a) and continued to be higher through the end of selection. The response to selection reached a plateau at generation 2, which may indicate that the dispersal response of *P. persimilis* has a very simple genetic architecture and that phenotypic variation in this trait is caused largely by variation in a small number of genes and not the environment. There was significant differentiation between the low-dispersal line and the unselected control by generation 1 ($F_{1,148} = 5.48$, $P = 0.02$; Fig. 3b); but there were no differences in generation 2 ($F_{1,66} = 0.02$, $P = 0.89$). Differences were observed at generation 3 ($F_{1,102} = 5.13$, $P = 0.03$) and continued through the 6-generation period ($F_{1,113} = 8.19$, $P = 0.005$, Fig. 3b). The relaxation experiment indicated that the high-dispersal line had a higher dispersal rate than the control population even after selection was relaxed ($F_{1,78} = 25.28$, $P < 0.0001$, mean time to disperse \pm SE, high line: 10.22 ± 2.97 ; control: 40.49 ± 2.97). The low-dispersal line did not show a loss in phenotypic value of the trait compared to the control population after relaxation of selection ($F_{1,70} = 18.42$, $P < 0.0001$, mean time to disperse \pm SE, low line: 22.66 ± 1.77 ; control: 9.45 ± 2.50).

In the second selection experiment, the high-dispersal line was again significantly higher than the control after one generation and continued until the end of the experiment ($F_{1,79} = 48.92$, $P < 0.0001$; Fig. 3a). Further, the second replicate of the high-dispersal line was not significantly different from selection replicate I at the end of the experiment ($F_{1,118} = 2.61$, $P = 0.10$; Fig. 3a, mean time to disperse \pm SE, high line selection regime I: 10.20 ± 0.47 , high line selection regime II: 11.38 ± 0.57). Estimates of realized

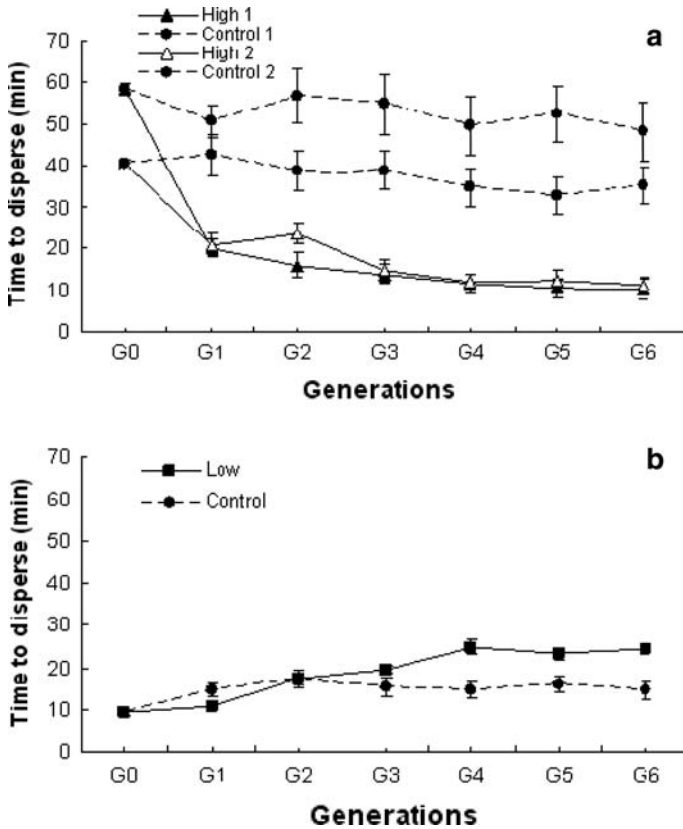


Fig. 3 Mean (\pm SE) dispersal response per generation for *P. persimilis* subjected to **a** selection for high-dispersal and **b** selection for low-dispersal

heritability were significant for both the high- and low-dispersal lines. In contrast to other foraging traits, heritability was greater in the low line than the high line (Table 1). Realized heritabilities for high-dispersal lines were comparable between the two selection regimes (Table 1; Supplementary Fig. 4).

Olfactory response

As with dispersal lines, the high-and low-olfactory response lines were selected under different test conditions. We maintained controls for both test conditions by which predator response to clean or uninfested plant volatiles (i.e., plants on which there were no prey) was assayed to differentiate between random movement in the presence of uninfested volatiles and olfactory sensitivity in the presence of prey-infested volatiles. There was no significant differentiation between the high olfaction line and the unselected control by generation 1 ($F_{1,16} = 2.62$, $P = 0.13$; Fig. 4a). However, differences were observed in generation 2 ($F_{1,14} = 5.22$, $P = 0.04$) until the end of the six generation period ($F_{1,11} = 12.96$, $P = 0.004$; Fig. 4a). There was significant differentiation between the low-olfaction line and the unselected control in generation 1 ($F_{1,13} = 7.02$, $P = 0.02$; Fig. 4b); but no significant differences were observed at the end of the selection

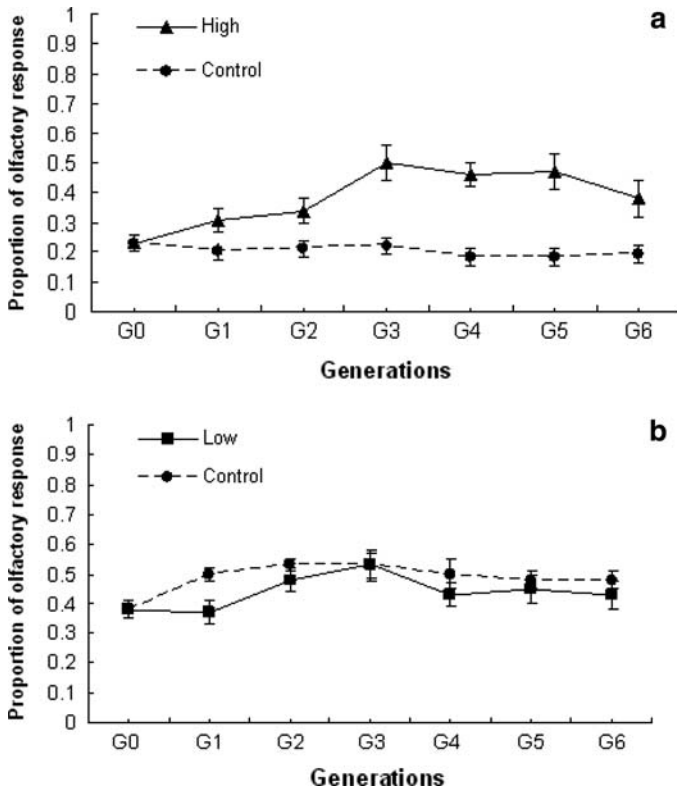


Fig. 4 Mean (\pm SE) olfactory response per generation for *P. persimilis* subjected to selection for **a** high-olfactory response and **b** low-olfactory response

experiment ($F_{1,7} = 3.04$, $P = 0.13$; Fig. 4b). We suggest that the majority of the phenotypic variation in olfactory behavior is caused by environmental and not genetic effects.

The high-olfactory response line reverted back to pre-selection levels after relaxation of selection ($F_{1,7} = 2.01$, $P = 0.19$; mean percentage response \pm SE for the high line was 0.25 ± 0.02 , and for the control 0.18 ± 0.03). The low-olfactory response line was not different from the control population after relaxation of selection ($F_{1,6} = 3.43$, $P = 0.11$; mean percentage response \pm SE for the low line was 0.38 ± 0.04 , and for the control 0.48 ± 0.04). Consistent with the slow selection response, the heritability estimates were much lower for the olfactory response lines than the other foraging traits, indicating that most of the variability in the olfactory response resulted from factors other than additive genetic variance (Table 1). The realized heritability estimate for the low-line was not significant (Table 1; Supplementary Fig. 5).

Indirect responses to selection

Foraging traits

Response of consumption to selection on other traits Bidirectional selection on conversion efficiency, dispersal or olfactory response did not affect prey consumption compared

to the unselected control population ($F_{2,25} = 0.00$, $P = 0.99$; $F_{2,23} = 0.06$, $P = 0.94$; $F_{2,25} = 0.22$, $P = 0.814$; respectively).

Response of conversion efficiency to selection on other traits The low-consumption line had higher conversion efficiency than the high-consumption line and unselected control population (mean conversion efficiency \pm SE, high line: 0.11 ± 0.05 ; low line: 0.14 ± 0.05 ; control population: 0.12 ± 0.005 ; $F_{2,24} = 7.34$, $P = 0.003$). Selection did not affect the conversion efficiency of the high- or low-dispersal lines ($F_{2,23} = 0.13$, $P = 0.87$) or olfactory response lines ($F_{2,25} = 3.61$, $P = 0.06$).

Response of dispersal to selection on other traits In contrast to the consumption and conversion efficiency lines, the high- and low-dispersal lines were selected under different test (prey density) conditions: 5 prey for the low line and 40 prey for the high line. Hence, the indirect response to dispersal under selection for consumption, conversion efficiency and olfactory response, including the unselected control, was calculated using a two-way ANOVA with effects of selection regime and prey density (5 or 40 eggs) in the model. The average leaving time of the unselected control population in the presence of 5 eggs was 25.00 ± 5.08 min and 40 prey eggs was 55.55 ± 5.61 min.

There was no significant interaction between selection regime and prey density in the dispersal response of high- and low-consumption lines ($F_{2,55} = 0.94$, $P = 0.39$). However, main effects, selection regime ($F_{2,55} = 5.86$, $P = 0.005$) and prey density ($F_{1,55} = 41.38$, $P < 0.0001$) had a significant effect on the dispersal response of the high- and low-consumption lines compared to the unselected control. The high-consumption line left the prey patch sooner (24.16 ± 2.59 min with 5 prey eggs, 46.29 ± 4.31 min with 40 prey eggs), and the low line stayed longer (34.54 ± 3.21 min with 5 prey eggs, 71.37 ± 9.04 min with 40 prey eggs) on leaf disk than did the control. Both lines dispersed sooner in the presence of 5 prey eggs than with 40 prey eggs. Selection regime did not affect the dispersal response of the conversion efficiency lines compared to the unselected control ($F_{2,54} = 0.52$, $P = 0.59$), hence conversion efficiency was not correlated with dispersal response. There was a significant two-way interaction between selection regime and prey density in the dispersal response of the olfactory lines ($F_{2,61} = 5.07$, $P = 0.009$). Regardless of number of prey available, the high-olfactory response line left a prey patch sooner (15.66 ± 2.72 min with 5 prey eggs, 21.16 ± 1.83 min with 40 prey eggs) than the low line (17.50 ± 2.10 min with 5 prey eggs, 34.33 ± 5.41 min with 40 prey eggs) and unselected control ($P < 0.0001$). Similar to the consumption lines, the olfactory response lines dispersed sooner in the presence of 5 eggs than 40 eggs.

Response of olfaction to selection on other traits The olfactory response lines were selected under two test conditions: high level of volatiles for the low line and low level of volatiles for the high line. We maintained a control whereby predator's response was assayed in the presence of uninfested plants to differentiate between random movement in the absence of prey-induced volatiles and olfactory sensitivity in the presence of prey-induced volatiles. A two-way ANOVA with selection regime including unselected control and volatile level in the model was used to test for correlated responses in olfaction.

There was a significant two-way interaction between selected lines and volatile level on the olfactory response of the consumption lines ($F_{2,24} = 6.63$, $P = 0.006$). The high-consumption line was positively correlated with olfactory response ($F_{1,24} = 19.90$, $P < 0.0001$; Table 2). The low line was comparable to the unselected control (Table 2).

Table 2 Indirect response of olfaction to bidirectional selection on other foraging traits including consumption, conversion efficiency and dispersal response

Trait	Infested volatiles (%)	Uninfested volatiles (%)
Consumption		
High line	0.72 ± 0.05	0.26 ± 0.03
Low line	0.32 ± 0.06	0.16 ± 0.04
Unselected control ^a	0.42 ± 0.05	0.16 ± 0.04
Conversion efficiency		
High line	0.70 ± 0.04	0.20 ± 0.03
Low line	0.46 ± 0.05	0.16 ± 0.03
Unselected control ^a	0.42 ± 0.05	0.16 ± 0.04
Dispersal response		
High line	0.50 ± 0.04	0.13 ± 0.03
Low line	0.20 ± 0.04	0.10 ± 0.04
Unselected control ^a	0.28 ± 0.05	0.13 ± 0.07

Values indicate mean ± SE proportion response of *P. persimilis* to *T. urticae*-induced plant volatiles in an air-still arena bioassay

^a The unselected controls was initiated from the same source population but tested at a different times

Olfactory response of the high- and low-consumption lines increased significantly in the presence of infested volatiles compared to clean volatiles ($F_{2,24} = 70.4$, $P < 0.0001$, Table 2). There was a significant effect of interaction ($F_{2, 24} = 17.48$, $P < 0.0001$) between selection and volatile level on the olfactory response of the conversion efficiency lines compared to the unselected control. The high-conversion efficiency line was positively correlated with olfactory response ($F_{2, 24} = 136.52$, $P < 0.0001$, Table 2). Again, the olfactory sensitivity of mites increased in the presence of volatiles but not to clean volatiles ($F_{1, 24} = 26.00$, $P < 0.0001$, Table 2). There was a significant selection × volatile interaction ($F_{2,18} = 7.83$, $P = 0.0036$) on the olfactory response of the dispersal lines compared to the unselected control. The high-dispersal line showed a positive correlation with olfactory response ($F_{2,18} = 9.85$, $P = 0.0013$, Table 2). The low-dispersal line had diminished olfactory response compared to the high line and unselected control (Table 2). The lines showed an increased olfactory response in the presence of infested volatiles compared to clean volatiles ($F_{1,18} = 44.52$, $P < 0.0001$, Table 2).

Life-history traits and intrinsic rate of increase

Response of hatching time and percent hatch to selection on foraging traits

Selection had no significant effect on the hatching time (days) of the consumption lines ($F_{2,102} = 0.28$, $P = 0.75$), conversion efficiency lines ($F_{2,111} = 1.05$, $P = 0.35$), dispersal lines ($F_{2,107} = 1.95$, $P = 0.14$) or olfactory response lines ($F_{2,104} = 1.00$, $P = 0.37$) compared to the unselected control. The average hatching time in the unselected control population was 1.21 ± 0.08 days. Neither did hatching percent differ in the consumption lines ($F_{2,102} = 1.11$, $P = 0.33$), conversion efficiency lines ($F_{2,111} = 2.38$, $P = 0.09$), dispersal lines ($F_{2,107} = 1.01$, $P = 0.37$) or olfactory response lines ($F_{2,104} = 1.02$, $P = 0.36$) compared to the unselected control. The average hatching percent in the unselected control population was 94.73 ± 3.59 .

Response of development time to selection on foraging traits

Selection on consumption had a significant effect on the development time (days) from nymph to adult ecdysis ($F_{2,101} = 7.12$, $P = 0.001$). The low-consumption line had a slightly longer development time compared to high-consumption line and unselected control (mean development time \pm SE, high line: 3.00 ± 0.03 ; low line: $3.16 \pm .04$; unselected control population: 3.00 ± 0.03). Bidirectional selection on conversion efficiency ($F_{2,106} = 1.08$, $P = 0.45$), dispersal ($F_{2,105} = 1.98$, $P = 0.14$) and olfactory response ($F_{2,103} = 2.17$, $P = 0.11$) did not affect development time compared to the unselected control. The average development time in the unselected control was 3.00 ± 0.03 days.

Response of survivorship to selection on foraging traits

Bidirectional selection on consumption ($F_{2,81} = 0.29$, $P = 0.75$), conversion efficiency ($F_{2,81} = 0.83$, $P = 0.43$), dispersal ($F_{2,81} = 0.04$, $P = 0.96$) or olfactory response ($F_{2,81} = 0.49$, $P = 0.61$) did not affect the survivorship compared to the unselected control. The percentage survivorship for a cohort of predatory mites from the unselected control was 68.57 ± 3.66 .

Response of fecundity to selection on foraging traits

The high-consumption line had a significantly higher fecundity than the low-consumption line and the unselected control ($F_{2,66} = 54.67$, $P < 0.0001$, mean fecundity \pm SE: high line: 3.58 ± 0.12 ; low line: 1.86 ± 0.12). A similar result was obtained for the conversion efficiency lines ($F_{2,66} = 98.18$, $P < 0.0001$, mean fecundity \pm SE: high line: 3.51 ± 0.08 ; low line: 1.94 ± 0.08). Neither selection on dispersal nor on olfactory response affected fecundity ($F_{2,66} = 0.85$, $P = 0.43$, mean fecundity \pm SE: high line: 2.34 ± 0.08 ; low line: 2.12 ± 0.08 ; $F_{2,66} = 2.54$, $P = 0.08$, mean fecundity \pm SE: high line: 2.12 ± 0.08 ; low line: 2.03 ± 0.08). The average daily fecundity in the unselected control was 2.27 eggs.

Response of intrinsic rate of increase to selection on foraging traits

Bidirectional selection on consumption significantly affected the intrinsic rate of increase (r_m) compared to the unselected control ($F_{2,27} = 854.39$, $P < 0.0001$, Table 3). The high-

Table 3 Intrinsic rate of increase (r_m) \pm SE generated from jackknifed $l_x m_x$ data for cohorts of *P. persimilis* selection lines

Trait	r_m
High-consumption	0.429 ± 0.01
Low-consumption	0.298 ± 0.01
High-conversion efficiency	0.418 ± 0.008
Low-conversion efficiency	0.307 ± 0.008
High-dispersal	0.367 ± 0.002
Low-dispersal	0.369 ± 0.002
High-olfactory response	0.380 ± 0.002
Low-olfactory response	0.374 ± 0.002
Unselected control	0.375 ± 0.01

consumption line had a higher rate of increase than the low-consumption line and the control. Selection also affected the r_m of the conversion efficiency lines compared to the unselected control ($F_{2,27} = 569.43$, $P < 0.0001$; Table 3). The high-conversion efficiency line has a higher r_m than the low line and control. Selection on dispersal or olfactory response did not affect r_m compared to the unselected control line ($F_{2,27} = 2.88$, $P = 0.07$; $F_{2,27} = 1.63$, $P = 0.21$ respectively; Table 3).

Discussion

Direct response to selection: heritability and stability

Foraging is composed of multiple, interacting behavioral and physiological components (Stephens and Krebs 1986; Sokolowski 2001). An evolutionary perspective on foraging raises fundamental questions about the processes that influence the nature and maintenance of genetic variation in these phenotypic components in natural populations (Lande and Arnold 1983; Arnold 1986). In the present study, we quantified the amount of genetic variation and correlations in multiple traits to determine their influence on the rate and direction of evolution of foraging phenotypes in the predatory mite, *P. persimilis*. Several studies have investigated the genetic basis of foraging [i.e., in cave fish (Schemmel 1980), snakes (Arnold 1981), mice (Gray 1980), and *Drosophila* (deBelle and Sokolowski 1987), honey bees (Page et al. 1995), and other insects (Futuyma 1983; Tauber and Tauber 1987; Gu and Danthanarayan 1992)]. However, these studies considered only one aspect of foraging so their measurements of heritable variation provide a more limited description of the possible evolution of complex foraging phenotypes than does ours.

Many predators forage in variable, unpredictable environments. Under these conditions, wide phenotypic variation in foraging traits is expected (Southwood 1977). In fact, all four of the foraging traits we evaluated (prey consumption rate, conversion efficiency, dispersal and prey-finding by olfaction) exhibited such variation (Supplementary Fig. 1) and, with the exception of the olfactory response lines, showed steady and rapid divergence between the high and low lines under selection. These results suggest, that much of the phenotypic variation in predator foraging traits may be attributed to a modest number of loci with relatively large phenotypic effects (Macnair 1990; Falconer and Mackay 1996; Orr 1998), which agrees with an estimate derived from crosses between inbred lines (Jia et al. 2002). Heritability is of central importance in theories of phenotypic evolution because the selection response is proportional to heritability as well as to the intensity of selection (Falconer and Mackay 1996). The only trait for which we did not find significant heritability was the low olfactory response. Genetic analyses of olfactory response have also reported low heritability estimates ($h^2 = 0.08$ – 0.25) in *Drosophila melanogaster* Meigen (Mackay et al. 1996), and a parasitic wasp, *Cotesia glomerata* (L.) (Wang et al. 2003). Low heritability is consistent with two hypotheses; either strong selection has depleted genetic variation in the population (Merilä et al. 2001) or the traits are very sensitive to environmental influences (Falconer and Mackay 1996). Although we cannot distinguish between these two possibilities, we expect the latter is more likely in the case of the olfactory response because plant production of herbivore-induced volatiles varies widely and rapidly depending on season, time of day, plant age and plant part (Dicke et al. 1990a; Takabayashi et al. 1994). Thus, olfactory response might be more plastic than the other traits to cope with the complexity and variability of plant production of volatiles (Vet et al. 1995).

In contrast to the very low heritability of olfactory behavior, the heritability estimates of consumption, conversion efficiency and dispersal response were significant and much larger than what is sometimes expected for behavioral traits in animals (Mousseau and Roff 1987; Plomin 1990), although estimates of heritability for behavioral traits in the literature may generally be unrealistically low (Hoffman 2000). Our results are consistent with previous estimates of these traits (Margolies et al. 1997; Jia et al. 2002), and are further supported by the consistency of response to both selection regimes. Furthermore, heritability estimates for behavioral traits, including dispersal-related traits, in insects are often reported to be high, $h^2 = 0.5$ or more (Dingle 1991; Gu and Danthanarayan 1992; Keil et al. 2001; Roff and Fairbairn 2001 and references therein). It is remarkable that we detected consistently high heritabilities and rapid selection responses for three out of the four components of foraging, which were investigated in both the first and second selection regimes. This suggests that in the absence of significant genetic constraint these foraging traits can respond rapidly to selection.

The high heritabilities we found could mean that the traits are not under strong selection or that they are under strong selection but the direction of selection varies over time. *Phytoseiulus persimilis* generally reside in a highly variable environment (Sabelis and Dicke 1985) in which changing density and distribution of prey is likely to affect foraging success. In our study we investigated genetic variation and the response to selection on this variation in the production of phenotypes because we feel that rapid selection is likely to be the most important for short-lived organisms in variable environments in nature. Varying resource levels may affect the strength as well as the direction of selection (McPeck and Holt 1992). Thus, the evolutionary optima for foraging changes frequently, and a genetic system that responds quickly to this variation would facilitate the rapid response of populations to changes in the environment (i.e., prey abundance). However, selection is not the only mechanism available to deal with changing environments. For example, phenotypic plasticity may allow individuals to alter their foraging phenotypes within an individual's lifespan to deal with changing environmental conditions (Vet and Dicke 1992; Sabelis and Janssen 1993; Poppy et al. 1997; Kause et al. 1999; Sambandan et al. 2008). However, for the *P. persimilis*–*T. urticae* interaction we think that the influence of genetic variation would outweigh the significance of plasticity because the lifespan of the predatory mite (20–30 days; Takafuji and Chant 1976) is short in comparison to the time scale for dynamic changes in prey availability (i.e., patches of *T. urticae* persist for 15–40 days in the presence of *P. persimilis*; Hance and Van Impe 1999). Thus, within an individual's lifespan the environment can be considered to be generally homogenous and relatively stable, but across generations it is likely to change dramatically resulting in variable patterns of natural selection over time.

Selection limits may occur in a population under artificial selection because of physical constraints associated with the assay or the character, i.e., how many prey a predator can handle in a time-limited trial (Holling 1961); evolutionary constraints, such as might occur if a trait is opposed by natural selection operating in the opposite direction directly on the trait or on some correlated traits; or because of genetic constraints where pleiotropy or tight physical linkage among the genes affecting two traits affect the rate and/or the direction of the selection response. We examined the latter two possibilities in two ways. First, we relaxed artificial selection on all foraging phenotypes to determine if natural selection (i.e., 10–12 generations of random mating without artificial selection) would reverse the response to selection. Second, we measured correlated responses to selection among the four foraging traits and various components of life histories. When selection was relaxed, all high foraging phenotypes, except the high-olfaction line, were phenotypically stable for

at least 2 months (10–12 generations), but among the low foraging phenotypes only the low-dispersal line remained stable. This stability (or lack of stability) of the selection response is consistent with the direction of artificial selection and fitness. That is, the lines that are stable after selection was relaxed should represent selection regimes that change fitness in the same direction as natural selection. This result is generally consistent with the change in fitness in the laboratory environment (i.e., r_m) observed among the selection lines relative to the unselected control lines (Table 3).

Indirect responses to selection

In nature, where predators must track spatially and temporally dynamic prey populations, long-term success depends equally on the ability of predators to exploit local prey populations and to find new prey patches (Abrams 2000; Ellner et al. 2001; Pels et al. 2002; Sabelis et al. 2005). These ecological associations predicted in theory should be reflected in genetic and phenotypic correlations between foraging traits and between foraging and life-history traits because of their joint impact on colonization and reproduction (Safriel and Ritte 1983; Parsons 1983). Therefore, traits that affect local prey use and those that affect prey finding might be correlated to maximize foraging efficiency. Foraging traits might also be correlated with life-history traits that enhance the ability of predator populations to persist in a new patch (Lewontin 1965; Simberloff 1981; Safriel and Ritte 1983). For example, dispersal behavior is often positively correlated with such traits as growth and fecundity (Roff 1986; Zera and Rankin 1989). However, other studies on foraging behaviors in predatory arthropods and parasitoids provide no evidence of such correlations (Wang et al. 2003; Maeda 2005, 2006). Most of the foraging traits we studied exhibited either small positive or no correlation with one another, and some of those correlations were likely not genetic (i.e., at high consumption rates there were higher frequencies of partial prey consumption, which, because of the formula used to calculate conversion efficiency, led to lower estimates of the latter). Similarly, we found no correlations between foraging traits and life-history traits with one exception, there was a negative correlation between low-consumption and development time. However, this statistical correlation might not translate to significant biological differences over the lifespan of the organism because variation in development time was so small.

These results suggest that the majority of the genetic control that underlie the phenotypic components that make up foraging behavior are largely non-overlapping, but the presence of some significant correlated responses to selection implies that pleiotropic effects partially contribute to the variation in foraging in the field. The presence of partially overlapping but not fully integrated genetic architectures among traits implies that certain axes of genetic variation that contain ample genetic variation will result in more rapid evolutionary responses, while axes of variation with little or no genetic variation will likely constrain or eliminate evolutionary responses (Schluter 1996). This is significant for species that reside in variable environments as the presence of genetic independence (or constraint) among traits will ultimately determine how fast populations will respond to variable selection pressures (Arnold and Phillips 1999).

Maintaining variation in foraging traits

The stability of the high foraging phenotypes, when viewed in light of the conditions under which the lines were maintained and assayed, offers insight into the maintenance of genetic variation in natural populations. All lines were reared on abundant prey throughout our

experiments, so there was no cost to extremely high consumption or reproduction in terms of resource depletion and the traits were maintained. In environments in which resources (i.e., prey) are homogeneous, individual predators are expected to maximize their immediate benefits even at the expense of long-term yields (Rosenzweig and MacArthur 1963; Maynard-Smith 1982). Thus, under laboratory conditions the high consumption and high conversion efficiency lines would benefit from their higher r_m and would be expected to increase at the expense of other phenotypes. However, we must then account for the high variance in the source populations. We hypothesize that habitat heterogeneity, in terms of prey density and location is the likely cause of maintenance of genetic variation in *P. persimilis* foraging traits. The availability of spider mites varies dramatically with space and time (Jeppson et al. 1975; Sabelis et al. 1991). This spatial and temporal variation in the environment produces dynamic changes in the selective optima. Predatory mites must deal with the potential conflicts that arise in allocating time and energy to different foraging demands, especially when resources become scarce. Predators with high consumption or high conversion efficiency may be at a selective disadvantage because they do not make full use of the prey's growth capacity and hence produce fewer offspring (van Baalen and Sabelis 1995). Our data suggest that predators will be able to respond to these conditions as a result of highly heritable and relatively unconstrained genetic control for four components of foraging phenotypes.

Theoretical (Barton and Turelli 1989; Goldstein and Holsinger 1992) and empirical (Denno et al. 1991) work suggests that if different genotypes exist and each is favored by different environments, then genetic variation can be maintained by spatially fluctuating environments. Temporally fluctuating environments also may maintain genetic variation (Mackay 1981; Gillespie and Turelli 1989) by opposing selection on the trait in question. The resulting heterogeneity of foraging environments favors the coexistence of different genotypes because no single genotype can produce an average phenotype that is optimal in all environments (Gillespie and Turelli 1989). A central assumption in foraging theory is that strategies for the exploitation of patchily distributed resources are closely related to the reproductive success or fitness of foraging organisms (Stephens and Krebs 1986). Although we found no difference in the r_m of the high- and low-dispersal and olfactory response lines compared to the unselected control population, it does not necessarily follow that the former lines will not be successful in natural environments. This may explain how and why variation in foraging traits occurs in populations of predatory mites. Reproductive success may depend critically on how well a foraging strategy is attuned to the distribution of resources across spatial scales. In other words, different conditions may favor *P. persimilis* that exhibit a foraging strategy based on a strong or weak foraging response in consumption, conversion efficiency, dispersal and olfaction. To reveal the factors that determine the foraging strategies of *P. persimilis* it will be necessary to systematically examine the effect of specific foraging traits under different conditions of prey abundance and distribution.

Acknowledgments We thank X. Wu, N. Timmons and Y. Jia for helping with mite counts and maintenance of mite colonies. We also acknowledge Dr. Jeremy Marshall for his review of an earlier draft, and The Don C. Warren Genetic Fund for funding P. N. This is Contribution No. 09-113-J from the Kansas Agricultural Experiment Station, Manhattan, KS.

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