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Repeatability of Aggressiveness against Con-and Heterospecific Prey in the Predatory Mite *Neoseiulus californicus* (Acari: Phytoseiidae)

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ABSTRACT

Repeatability, (the consistency with which a given trait is expressed) of aggressiveness against prey (attack latency) in gravid females of the predatory mite *Neoseiulus californicus* (McGregor) was examined. In two experiments, prey - conspecific individuals, the onion thrips *Thrips tabaci* (Lindeman), and the two-spotted spider mite *Tetranychus urticae* Koch- were repeatedly offered in various no-choice *vs.* choice situations. Throughout the first experiment, the predators were offered conspecific larvae twice, alone and then together with *Te. urticae*. In a second experiment, the predators were alternately offered *Te. urticae* and *Th. tabaci* within choice *vs.* no-choice situations. Latency to the first successful attack (resulting in death and consumption of prey) was recorded as aggressiveness. In the first experiment, Pearson's r indicated that the predators were consistent in aggressiveness against conspecific prey. Additionally, latency to attack conspecific larvae and *Te. urticae* were strongly correlated when the former were offered alone and the latter offered together with conspecific larvae. In the second experiment, aggressiveness against spider mites and thrips was inconsistent, non-repeatable and varied among contexts. However, *Te. urticae* was attacked more quickly when offered second, following the first prey *Th. tabaci* than when offered as the first prey. Both experiments, in concert, suggest that the level of behavioral consistency of *N. californicus* in aggressiveness against prey is strongly context-dependent. Further in-depth studies are needed to determine which foraging traits, (and why and under what circumstances) are more repeatable than others.

Keywords: Aggressiveness, Cannibalism, Consistency, *Neoseiulus californicus*, Repeatability.

INTRODUCTION

Heritable differences among individuals are essential elements of natural selection (Darwin, 1859). The evolution of behavioral traits, like the evolution of any other trait, is a result of both selection on phenotypic variation and inheritance of the variants (Fisher, 1958). For an assessment of the potential strength of selection for a given trait, one can quantify the consistency with which a given trait, for example food preference, is expressed. Consistency of a given trait can be assessed using repeatability (Lessells and Boag, 1987; Harper, 1994; Wolak *et al.,* 2012). Consistent individual differences in behavior are quantified by measuring a given behavioral trait of individuals on more than one occasion and in several contexts. Thus, for an assessment of individual feeding preferences, this trait should be evaluated repeatedly in different contexts. Such data

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can then be utilized to calculate the repeatability of the preference. Indeed, repeatability is an estimation of the proportion of variations among individuals, which is due to individual differences (Falconer and Mackay, 1996). The repeatability concept comes from quantitative genetics theory describing the degree to which variation within individuals contributes to total variation in a population. It provides information regarding whether individuals differ sufficiently for selection to act on and may be a particularly useful measure of variation for behavioral ecologists because of its possible implications to heritability of behavioral traits. In order for preferences (e.g. in foraging contexts) to evolve, individuals must show heritable genetic variation either in this preference or in their learning ability, which, in turn, is expected to result in phenotypic differences among individuals.

Estimates of repeatability of a behavioral trait are useful for at least three reasons. First, despite the standard definition of repeatability by Falconer and Mackay (1996), some reports state that repeatability sets an upper limit to our ability to detect heritability (Becker, 1984; Boake, 1989). Second, these estimates will indicate to what extent behavioral traits are influenced by experience and/or non-genetic inheritance, such as maternal effects (Bernardo, 1996). Third, high repeatability values indicate that individuals tend to perform consistently, making multiple measurements negligible (Arnold *et al.,* 1995; Falconer and Mackay, 1996). Bell *et al.* (2009) recently conducted a meta-analysis of repeatability based on repeated observations of a single behavioral trait of the same individual and found that most published repeatability values [calculated through ANOVA approach (Harper, 1994)] ranged between 0.1 and 0.2, with 1 signifying complete heritability. Consistent differences in various behavioral traits have been demonstrated in a wide range of invertebrates and as well in vertebrates, ranging from insects and spiders to fish, reptiles, birds and mammals (for review: Pruitt and Riechert, 2011; Laskowski and Bell, 2013; Sih *et al.,* 2004; Bell *et al.,* 2009; Brodie and Russell, 1999; Dall *et al.,* 2004).

Repeatability of aggressiveness against prey in the plant-inhabiting predatory mite *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae), which is a generalist predator of plant-inhabiting mites and insects, was assessed. Preys used were conspecific larvae, the two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae) and the onion thrips, *Thrips tabaci* (Lindeman) (Thysanoptera: Thripidae). *Tetranychus urticae* is globally recognized as an important polyphagous herbivorous pest (Migeon and Dorkeld, 2010). *Thrips tabaci* is an oligophagous pest, feeding on various vegetable and ornamental plants (Trdan *et al.,* 2007). Among plant-inhabiting predatory mites, phytoseiids are the most studied because of their importance in the control of phytophagous mites on agricultural crops (Helle and Sabelis, 1985). *Neoseiulus californicus* is one of the main natural enemies used in biological control of the above mentioned two pests (McMurtry, 1977; McMurtry and Croft, 1997) and has been widely used via inundative and inoculative release in America and Europe (Swirskii *et al.,* 1970; Oatman *et al.,* 1977; Picket and Gilstrap, 1986; Castagnoli and Simoni, 1991; Raworth *et al.,* 1994; Jolly, 2000; Croft *et al.,* 1998). The present study presents a first attempt to study the repeatability of a given behavioral trait in predatory mites by examining the repeatability of aggressiveness of *N. californicus* against prey.

MATERIALS AND METHODS

Predator and Prey Rearing

The laboratory population of *N. californicus* was founded with specimens originally obtained from Koppert (NL) and was reared on detached leaves of Common

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Bean, *Phaseolus vulgaris* L., infested by two-spotted spider mites, *Te. urticae* (TSSM), and pollen of maize, *Zea mays*. Detached leaves were piled up on artificial arenas consisting of a tile resting on a water-saturated foam cube kept in a plastic box half-filled with water. Moist tissue paper was folded over the edges of the tile to prevent the mites from escaping. To obtain predator eggs used in the experiments, gravid females were randomly withdrawn from the laboratory population, transferred to detached leaf arenas and provided with mixed life stages of spider mites. Each leaf arena was constructed of a leaf placed upside down on a water-saturated foam cube kept in a plastic box half-filled with water. Moist tissue paper was wrapped around the stem of the leaf to maintain leaf turgidity and folded over its edges to prevent mites from escaping. Eggs laid by the predator females were collected every 24 hours to be used in the experiments. Mobile immature spider mites used as prey in experiments were randomly collected from a population reared on whole bean plants, *P. vulgaris*. To obtain the first instar larvae of onion thrips, *Th. tabaci* (TT), used as prey in the experiments, adult female thrips were reared on cucumber leaves (*Cucumis sativus* L.) and allowed to lay eggs. Then the emerging first instar larvae were taken to be used in the experiments. Predator rearing units, leaf arenas and experimental cages were kept in a climate chamber at 25±1°C, 75±5% RH and 16:8 h (L: D) photo-period.

Experimental Procedures

In the first experiment even-aged eggs of *N. californicus* were obtained by placing gravid females on spider mite-infested detached bean leaves. Every 24 hours, newly laid eggs were collected. The immature predators were reared on maize pollen. Upon reaching adulthood (~4 to 6 days after being hatched) the sex of the predators was determined and each predator female was provided with a male (randomly taken from the laboratory population) for 24 hours. Experiments were carried out using artificial cages each consisting of a circular cavity of 20 mm diameter and 6 mm height with fine gauze at the bottom and closed on the upper side by a microscope slide (Schausberger, 1997). Single mated females (28 replicates) were isolated in these cages and presented prey therein. Gravid females were used as experimental animals because they are of the highest prey needs among all their life stages and phases, and are thus expectably the most aggressive individuals. Aggressiveness of each female, defined as latency to attack prey, was assessed on four dates (3, 6, 10 and 15 days after reaching adulthood). Mobile immatures of TSSM and larvae of *N. californicus* (NC) were used as prey. Eggs of *N. californicus* to be used as prospective prey were transferred to a leaf arena of no TSSM. Hatched larvae were collected and used as conspecific prey. The sequence and number of prey offered to each predator female during this experiment was: 1st prey offering (day 3) 3 TSSM, 2nd prey offering (day 6) 3 NC larvae, 3rd prey offering (day 10) 3 NC larvae, and 4th prey offering (day 15) 3 TSSM and 3 NC larvae (choice test). In between the four assessments, the predators were fed on pollen. Immediately upon offering prey, latency to the first successful attack (resulting in death and consumption of prey) was recorded by monitoring the cages every 5 minutes during the first 2 hours and then within 30 minutes intervals during the next 6 hours.

The protocol of the second experiment was identical to that of the first experiment, except for the otherwise stated below: even-aged mated females were subjected to one of two treatments, with aggressiveness of each female assessed on days 2 and 6 after reaching adulthood. First instar larvae of *Th. tabaci* (TT) and mobile immatures of TSSM as prey were frozen at -20°C for 2 hours before being used in the experiment. Frozen killed prey were used instead of alive prey to exclude any inadvertent effect of vigor of the female, possibly differing and changing among treatments and over time, on their

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ability to overwhelm the prey. The sequence of prey provided was in the 1st treatment: (day 2) 3 TSSM, (day 6) 3 TT, (day 10) 3 TSSM, (day 14) 3 TT; in the 2nd treatment: (day 2) 3 TT, (day 6) 3 TSSM, (day 10) 3 TT, (day 14) 3 TSSM; in the 3rd treatment: (day 2) 3 TSSM, (day 6) 3 TT, (day 10) 3 TSSM and 3 TT (choice test); and in the 4th treatment: (day 2) 3 TT, (day 6) 3 TSSM, (day 10) 3 TSSM and 3 TT (choice test). Several individuals died before the end of the experiment resulting in a final replicate number of at least 13 females per treatment.

Approaches Estimating Repeatability

A variety of statistics have been applied to estimate the behavioral consistency or repeatability, such as Pearson's correlation coefficients (Hayes and Jenkins, 1997), the procedure proposed by Bland and Altman (1986), Maximum Likelihood (Mansour et al., 1981), and the ANOVA method (e.g. Harper, 1994). Computation of repeatability is thoroughly discussed, with examples, by Lessells and Boag (1987). Harper (1994) published a critical notion that correlation analysis is an improper method to test behavioral consistency/repeatability. However, if the ranking of individuals in two measurements is significantly positively correlated this is certainly an indicator of behavioral consistency. Moreover, one principle for the ANOVA approach advocated by Harper (1994) is that two successive measurements have to be independent, which is not the case if an individual is twice taken into account. Wolak *et al.* (2012) compared the advantages and disadvantages of various methods used to measure repeatability and indicated that the ANOVA approach does not account for the sequence of measurements. However, numerous studies on learning in the context of foraging behavior in various animals clearly suggest that the sequence of measurement does matter (Jensen and Yngvesson, 1998). Therefore, in this study Pearson's correlation coefficients were employed to assess the repeatability.

Statistical Analyses

Data from experiments 1 and 2 were separately analyzed using SPSS 18.0 (SPSS 2010). In experiments 1 and 2 within each treatment, between days' comparison of latency (to attack prey) was made through Generalized Estimating Equations (GEE; autocorrelation structure between days, posthoc pairwise comparisons through LSD). Similarly, in experiment 2 latency to attack prey on days 2 and 6 (treatments 1 and 3 *vs.* 2 and 4, respectively, combined) as affected by prey species and day were analyzed through GEE (autocorrelation structure between days, posthoc pairwise comparisons through LSD) (Hardin and Hilbe, 2003). Pairwise Pearson correlation coefficients (r) were computed to assess the repeatability of latency to attack prey, i.e. aggressiveness, in both experiments and within each treatment. In both experiments, data were normally distributed (Kolmogorov–Smirnov: $P > 0.05$) and exhibited homogeneous variances (Levene tests: $P > 0.05$).

RESULTS

First Experiment

Across the experiment, 83% of adult females survived until the end of the experiment. Day had a significant effect on latency to attack prey (GEE; Wald $X^2_3 = 39$, $P < 0.001$). There was no significant difference observed between the 1st and 4th prey offerings (Table 1; LSD: $P = 0.143$), indicating that prior experience with *Te. urticae* did not change aggressiveness of predator females against this prey on day 15 (choice test) (Table 1). However, there were significant differences observed between the 2nd and 3rd prey offerings (Table 1; $P < 0.001$) and also between any two of these

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Table 1. Latencies to attack prey (aggressiveness) of adult *N. californicus* females (min; Mean±SE) in the first experiment. Each female was subjected to four tests (prey offerings).

Prey offerings	Prey [a]	N	Mean ± SE [b]	Min	Max
1	TSSM	28	34.29 ± 2.02[c]	30	60
2	NC larvae	27	242.22 ± 34.52[a]	30	480
3	NC larvae	26	125.77 ± 22.93[b]	30	480
4	TSSM+NC larvae	24	40.00 ± 4.29[c]	30	120

[a] TSSM for *Te. urticae*, NC for *N. californicus*; [b] Different superscript letters accompanying means indicate significant differences between prey offerings (P< 0.05).

offerings and as well the 1st and 4th offerings (Table 1). Cannibalism-experienced predator females (in the 3rd prey offering) attacked conspecific larvae about two times earlier than cannibalism-naive females (in the 2nd prey offering) did (Table 1; P< 0. 001). In the 4th test, where the predatory mite females were offered a choice between conspecific larvae and *Te. urticae*, all females first attacked *Te. urticae*. Latency to attack on conspecific larvae and *Te. urticae* were strongly correlated between the 3rd and 4th prey offerings (Pearson's r= 0.67, P< 0.001) but not between the 2nd and 4th (r= 0.29, P= 0.17). Individual females were consistent in aggressiveness against conspecific prey in the 2nd and 3rd prey offerings (r= 0.557, P= 0.003). Overall, 7 out of 27 females did not attack the conspecific larvae in the 2nd prey offering within 8 hours, but 6 of these 7 females attacked conspecific within the 3rd prey offering.

Second Experiment

In the 1st and 2nd treatments ~70% and in the 3rd and 4th treatments ~60% of the adult females survived until the end of the experiment. Generalized Estimating Equation (GEE) on attack latency on days 2 and 6 revealed an interaction between day and prey but no main effects of these two variables (For prey: Wald X^2_1= 0.49, P= 0.48; For day: Wald X^2_1= 2.29, P= 0.13; For prey×days: Wald X^2_1= 4.00, P= 0.04). *Tetranychus urticae* was attacked more quickly on day 6 than on day 2 whereas there was no such effect for *Th. tabaci* (Figure 1). It thus seems that when the predators were first presented *Th. tabaci* and then *Te. urticae*, they were more aggressive against *Te. urticae* than when they were first presented *Te. urticae* and then *Th. tabaci* (Wald X^2_1= 307.13, P< 0.001). Within the 3rd treatment, 7 out of 14 adult females each attacked first *Te. urticae* and *Th. tabaci*, respectively, on day 10. In the 4th treatment, 6 out of 13 adult females attacked first *Te. urticae* on day 10 and 7 attacked first *Th. tabaci* (Table 2). Regarding repeatability within each treatment, there was no significant correlation observed between any of the latency to attack prey (Table 3; 1st treatment: all r< 0.26 and P> 0.29; 2nd treatment: all r< 0.31 and P> 0.26; 3rd treatment: all r< 0.25 and P> 0.37; 4th treatment: all r< 0.17 and P> 0.48). GEE between days within each treatment showed that in the 3rd and 4th treatments the predators attacked prey more quickly on day 10 than on days 2 and 6 (for 3rd treatment: Wald X^2_2= 25.7, P< 0.001; for 4th treatment: Wald X^2_2= 13, P= 0.001).

DISCUSSION

The overall, aggressiveness of *N. californicus* against prey was low and only in certain contexts repeatable. The first experiment suggests that adult females of *N. californicus* are consistent in aggressiveness in cannibalism, indicated by the positive correlation between the females' responses to conspecific larvae presented in two

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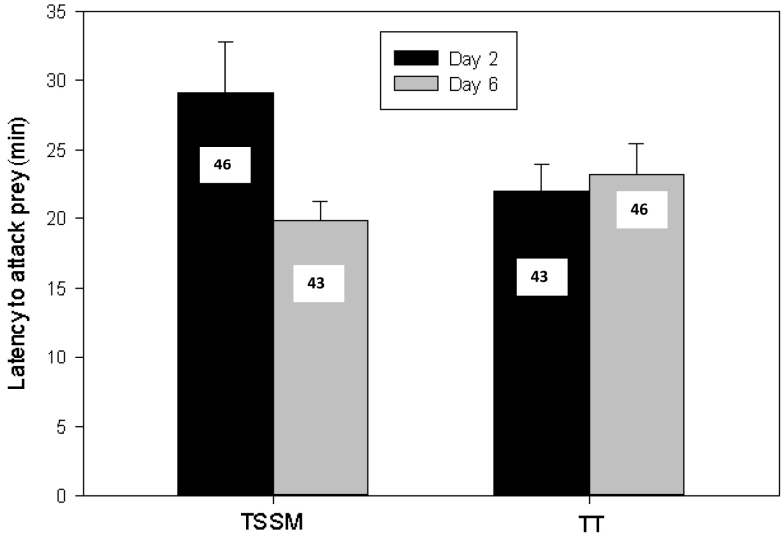

Figure 1. Time elapsed (mean + SE) until adult *N. californicus* females successfully attacked *Te. urticae* (TSSM) and *Th. tabaci* (TT) within 8 h after offering prey on days 2 and 6 of the second experiment. Numbers inside bars are the number of replicates.

Table 2. Latencies to attack prey (aggressiveness) of adult *N. californicus* females (min; Mean±SE) on *Te. urticae* (TSSM) and *Th. tabaci* (TT) in the second experiment. Each female was subjected to three (3rd and 4th treatment) or four (1st and 2nd treatment) tests.

	Day[a]	Prey	N	Attack latencies
1st treatment	2	TSSM	24	33.13±6.57
	6	TT	19	25.00±3.37
	10	TSSM	17	20.59±2.84
	14	TT	17	22.06±1.87
2nd treatment	2	TT	21	23.57±2.93
	6	TSSM	19	21.05±2.14
	10	TT	16	17.81±2.45
	14	TSSM	15	21.33±2.31
3rd treatment	2	TSSM	22	24.77±2.74
	6	TT	21	21.43±3.25
	10	TSSM	7	11.42±2.10
	10	TT	7	10.00±2.44
4th treatment	2	TT	22	20.45±2.41
	6	TSSM	18	18.61±1.60
	10	TSSM	6	10.00±2.58
	10	TT	7	10.71±2.02

[a] In the 3rd and 4th treatment on day 10 TSSM and TT were presented simultaneously and times for the first attacked prey are reported.

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Table 3. Repeatability (Pearson's *r*) of aggressiveness of adult *N. californicus* females against *Te. urticae* (TSSM) and *Th. tabaci* (TT) in the second experiment.

	Day	Prey	N	Comparison between days	r	P
1st treatment	2	TSSM	24	2,6	0.255	0.292
				2,10	0.144	0.583
				2,14	-0.213	0.412
	6	TT	19	6,10	0.260	0.313
				6,14	-0.128	0.625
	10	TSSM	17	10,14	-0.256	0.321
	14	TT	17	----	----	----
2nd treatment	2	TT	21	2,6	0.272	0.261
				2,10	0.159	0.556
				2,14	0.231	0.407
	6	TSSM	19	6,10	0.077	0.777
				6,14	0.310	0.261
	10	TT	16	10,14	0.228	0.414
	14	TSSM	15	----	----	----
3rd treatment	2	TSSM	22	2,6	0.094	0.686
				2,10	-0.256	0.377
	6	TT	21	6,10	-0.013	0.946
	10	TSSM+TT	14	----	----	----
4th treatment	2	TT	22	2,6	-0.175	0.488
				2,10	0.096	0.755
	6	TSSM	18	6,10	-0.116	0.706
	10	TSSM+TT	13	----	----	----

different tests. Moreover, aggressiveness was consistent between the pure cannibalism tests and the choice test where all females first attacked the spider mites. Thus, in the first experiment aggressiveness was consistent (repeatable) in different contexts under the premise that conspecific individuals were present. Throughout the second experiment, the predator females' aggressiveness against spider mite and thrips prey was inconsistent and variable among contexts, with the shortest attack latencies against *Th. tabaci* and *Te. urticae* in choice tests of the 3rd and 4th treatments. In these treatments, the females were more aggressive against the non-preferred prey *Th. tabaci* in choice than no-choice tests, which was also true for the preferred prey *Te. urticae*. This may either indicate that there were indeed differences in aggressiveness against the same prey type in choice and no-choice tests, or may simply be a consequence of the higher total number of preys offered in the choice tests.

The present repeatability estimates (Pearson's r) for aggressiveness of *N. californicus* in cannibalism contexts ranged between 0.29 and 0.67 for the first experiment, which is medium to high within-individual consistency for aggressiveness, and while 0.09 and 0.31 for the second experiment. Topically related studies on aggression or aggressiveness have been performed with various animals. For example, Cassady (2007) observed that greater aggression against other pigs was associated with improved performance in various other phenotypic traits. D'Eath (2004) showed that in domestic pigs, social experience improved consistency in

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aggressiveness over time and concluded that breeding or early life experiences could have long-lasting influences on aggressiveness. Gibbons et al. (2009) investigated consistency in behavior of dairy cows across time and situations (competition for a food resource) and observed that within-cow repeatability was highest for an aggressiveness index (r= 0.31). Bergmuller and Taborsky (2007) observed that in the fish *Neolamprologus pulcher* helpers engaging more in territory defense were consistently more exploratory and engaged less in territory maintenance. Here, aggressive displays were consistent within individuals and individuals displayed more often aggressively towards intruders when dominants were absent than when they were present.

Based upon evidence from a variety of animal species, some individuals are consistently more aggressive (Benus *et al.,* 1992) or more exploratory (Winkler and Leisler, 1999) than other individuals, and these consistent individual differences in behavior are often heritable (Bell, 2007; Kolliker, 2005) and may be related to fitness (Dingemanse and Reale, 2005; Smith and Blumstein, 2008). Although in the present study the predatory mites displayed some level of consistency in aggressive response across contexts in the first experiment, a lack of consistency observed in the second experiment indicates that *N. californicus* maintained a high level of plasticity in aggressiveness against prey. Low repeatability of a given trait, as observed in the second experiment, can be due to low heritabilities (Hoffmann, 2000). However, in general a number of genetic and environmental causes of variation among individuals need to be considered before being able to firmly conclude that there are no genetically based differences among them (Dohm, 2002). According to Hayes *et al.* (1998) low repeatability measures can be the result of a flawed protocol, or using a trait that is a set of age- or environment-specific traits as single independent trait. The low, non-significant estimates of repeatability of aggressiveness in the second experiment may partly be due to the relatively small sample sizes (Clusella-Trullas *et al.,* 2007) but gathering complete sequences, i.e. females subjected to no-choice and choice treatments, was difficult because some individuals died in between treatments, reducing the number of replicates in the 3rd treatment. Nonetheless, the initial number of replicates in the first and second experiment was similar suggesting that the differences in repeatability estimates depended mainly on the type of prey. Lacking repeatability in the second experiment suggests that the behavioral variations within individuals were mediated by such factors as prey type, physiological condition, and unknown aspects of the testing protocol. Behaviors with low repeatability are likely to respond to selection more slowly than behaviors that are strongly heritable and thus highly repeatable (Hoffmann, 2000). Behaviors with different levels of repeatability might evolve differently under the same strength of selection. Repeatability may also affect the relationship between expected fitness and phenotype (Stamenkovic-*Radak et al.,* 1992). Inconsistent behavioral traits will be expressed differently in different environments, and therefore will not have easily predictable fitness consequences. In *N. californicus*, such activities as foraging, commonly change or improve with experience (Rahmani *et al.,* 2009; Schausberger *et al.,* 2010, Peralta-Quesada and Schausberger, 2012), so they might show low repeatability. Selection on a given trait will be less effective when individuals are less consistent in this trait (Brodie, 1993) but in such cases, there may be strong selection on learning ability allowing to flexibly adjusting behaviors by experience. Experience is a factor that is very often not considered in experiments on repeatability (Wolak *et al.,* 2012). However, in foraging contexts, the sequence of prey offered may strongly influence aggressiveness, as also shown for *N. californicus* (Schausberger *et al.,* 2010).

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The relevance of prey sequence was also evident in experiment 2. In the first and second tests of the second experiment, the predator females were more aggressive against *Te. urticae* when they were first presented *Th. tabaci* and then *Te. urticae* than when they were first presented *Te. urticae* and then *Th. tabaci*. Similarly, in sparrows, *Junco hyemalis,* the females that first received the female intruder were more aggressive against both female- and male-conspecific intruders than females first receiving the male intruder, which were not very aggressive to either (Cain *et al.,* 2011). The differences in response to *Te. urticae* are intriguing but challenging to interpret. It could be that the predator females were either more hungry or more prone to attack their preferred prey after first feeding on *Th. tabaci* or sensitized by the presence of *Th. tabaci,* which is a potential offspring predator. When *Th. tabaci* was offered first, it may have been perceived by the predator female as a threat to her offspring, increasing her aggressiveness against prey in general. *N. californicus* larvae are highly vulnerable to predation by *Th. tabaci* (Walzer *et al.,* 2004). Sensitization by contact with *Th. tabaci* could also be an explanation for the fact that in the 3rd and 4th treatments of the second experiment the females, no matter whether they were first offered *Th. tabaci* and second *Te. urticae* or vice versa, were more aggressive against both *Th. tabaci* and *Te. urticae* in choice tests than in the previous no-choice tests.

CONCLUSIONS

Within the first experiment it was found that aggressiveness of *N. californicus* females against conspecific larvae and *Te. urticae* (when conspecific larvae were present) was correlated, indicating at least some level of repeatability. In contrast, within the non-cannibalism, heterospecific prey situations of the second experiment, aggressiveness was largely independent among different contexts and prey types, and apparently strongly influenced by such ontogenetic factors as learning, prey sequence, physiological state etc. Clearly, further studies are needed to determine the mechanistic basis of variation in aggressiveness to determine how and when selection does act on this behavior in predatory mites. Although some studies have dealt with learning, and its effect on foraging behavior of predatory mites (e.g. Rahmani *et al.,* 2009; Schausberger *et al.,* 2010; Peralta-Quesada and Schausberger, 2012), studying the repeatability of learning itself might be interesting by examining foraging in different habitats and questioning whether the process of learning is repeatable across habitat types.

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تکرارپذیری رفتار حمله‌وری علیه طعمه‌های همگونه و غیرهمگونه در کنه شکارگر *Neoseiulus californicus*(Acari: Phytoseiidae)

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چکیده

ما تکرارپذیری یا ثبات حمله‌وری علیه طعمه را در ماده‌های بارور کنه شکارگر *Neoseiulus californicus* (McGregor) بررسی کردیم. در دو آزمایش، افراد هم‌گونه شکارگر، تریپس پیاز و کنه تارتن دو لکه‌ای به صورت تکرار شده به عنوان طعمه در تست‌های انتخابی و غیر انتخابی ارائه شدند. در آزمایش اول، لارو هم‌گونه دو بار به تنهایی و سپس همراه با کنه تارتن دو لکه‌ای به شکارگر ارایه شد. در آزمایش دوم، تریپس پیاز و کنه تارتن دو لکه‌ای به صورت متناوب در تست‌های انتخابی و غیر انتخابی به شکارگر ارایه شد. مدت زمان سپری شده تا اولین حمله موفق (که منجر به مرگ طعمه شود) به عنوان حمله‌وری ثبت شد. در آزمایش اول، شاخص همبستگی پیرسون نشان داد که شکارگرها در حمله‌وری علیه طعمه هم‌گونه ثبات داشتند. افزون بر این زمانی که ابتدا افراد هم‌گونه و سپس کنه تارتن دو لکه‌ای ارایه می‌شد، حمله‌وری به این دو طعمه با هم همبستگی زیادی داشتند. در آزمایش دوم، حمله‌وری علیه کنه تارتن و تریپس بدون ثبات، بدون تکرارپذیری و نیز در زمینه‌های مختلف، متفاوت بود. همچنین، کنه تارتن دو لکه‌ای وقتی که به عنوان طعمه دوم بعد از تریپس پیاز ارائه شد، سریع‌تر از هنگامی که به عنوان اولین طعمه ارایه می‌شد، مورد حمله قرار گرفت. در کل آزمایش‌ها نشان دادند که حمله‌وری علیه طعمه در این کنه شکارگر در زمینه‌های مختلف متفاوت است. تحقیقات بیشتری نیاز است تا مشخص سازد کدام ویژگی‌های جستجوگری و در چه شرایطی بیشتر از سایر ویژگی‌ها تکرارپذیر هستند.

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