

MITES AS MODELS FOR EXPERIMENTAL EVOLUTION STUDIES

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(Received 21 May 2010; accepted 22 October 2010; published online 22 December 2010)

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ABSTRACT — Experimental evolution is a powerful tool to study the genetic and phenotypic changes in populations across generations and their potential causes. Due to their characteristics, mites represent an excellent group in which this methodology can be used. In this article, we review the literature on experimental evolution performed with mites as models. The studies we found focus on the evolution of host-plant selection, pesticide resistance, behavioral traits and sex-related traits. Overall, responses to selection were very rapid, and correlated responses on other traits were mostly absent or positive. We discuss the possible characteristics that make mites good models for experimental evolution studies and suggest future directions in the field.

KEYWORDS — experimental evolution; pesticide resistance; host-plant use; dispersal; diapause; sexual selection

INTRODUCTION

Experimental evolution refers to any study that measures the genetic and phenotypic changes of populations across generations, hence that follows the evolution of populations in real time. This methodology is the most powerful experimental tool to establish a causal link between evolutionary processes and adaptation patterns (Chippindale, 2006). This is due to three major characteristics: (1) knowledge of the ancestral state of the populations under study, (2) knowledge of the conditions imposed in different sets of populations leading to clear predictions to test evolutionary hypotheses, and (3) the ability to follow the dynamics of a pro-

cess, instead of measuring its end-product only. The methods of experimental evolution encompass a continuum ranging from artificial selection to laboratory natural selection (Chippindale, 2006). In studies of artificial selection, the experimenter defines a character that will be selected (*e.g.*, survival). The offspring of individuals carrying a character value above or below a certain threshold will be used to form the next generation, whereas that of other individuals will not. Given enough genetic variation, mean trait values in that population are expected to be modified after some generations.

This procedure allows to calculate the amount of genetic variation present in a population and to obtain a population with a desired trait value at the

end of the selection process. For these reasons, it has been widely used by plant and animal breeders. At the other extreme, laboratory natural selection (or quasi-natural selection (Kassen, 2002)) involves experiments in which organisms are let to evolve in a particular environment, but without any selection procedure being carried out by the experimenter. At the onset of the experiment, organisms are expected to be poorly adapted to the environment they are exposed to. In the following generations, individuals with genotypes more adapted to the environment than others will be over-represented. Again, given enough genetic variation in the population, after some generations individuals are expected to be on average more adapted to that environment than in the ancestral population. Whereas artificial selection attempts to identify the genetic properties of traits, laboratory natural selection aims to characterize the evolutionary responses of populations as a whole (Chippindale, 2006). Hence, individuals are not individually characterized as in artificial selection, but their differential reproduction (fitness) will define the possible evolutionary changes throughout generations.

The two main model organisms in this research area are the fruit fly *Drosophila melanogaster* and the bacteria *Escherichia coli* (Elena and Lenski, 2003). Several other organisms have been used in these studies, mainly insects, such as the house fly *Musca domestica* (Bryant and Meffert, 1995; Hurd and Eisenberg, 1975), the bean weevil *Acanthoscelides obtectus* (Tucic *et al.*, 1998; Tucic *et al.*, 1995), the seed beetle *Callosobruchus maculatus* (Fricke and Arnqvist, 2007), and micro-organisms, such as the yeast *Saccharomyces cerevisiae* (Anderson *et al.*, 2003), the paramecium *Paramecium caudatum* (Nidelet and Kaltz, 2007), the unicellular algae *Chlamydomonas* spp. (Reboud and Bell, 1997), other bacteria such as *Pseudomonas* spp. (Barrett *et al.*, 2005; Brockhurst *et al.*, 2003; Buckling *et al.*, 2003) and viruses (Turner and Elena, 2000). Some studies have been performed in *Arabidopsis thaliana* (Roux *et al.*, 2005) and in *Caenorhabditis elegans* (Cutter and Payseur, 2003; Lopes *et al.*, 2008). These organisms share characteristics that make them amenable to such studies, which are (1) easiness of maintenance in the lab, (2)

short generation times and (3) possibility to generate populations of large sizes. Most mite species also share these characteristics; hence they are potential good models for experimental evolution studies. Indeed, some studies have been performed on experimental evolution of mites, which we review here. Moreover, for the two main model organisms (*D. melanogaster* and *E. coli*) and a few others, there are several genomic resources available, which enables the characterization of the genotypic changes that underlie the phenotypic changes observed. Genomic tools are mostly lacking for mites. The recent advent of *Tetranychus urticae* as a model organism (Grbic *et al.*, 2007) has prompted the sequencing of the genome of this mite, as well as the gathering of several genomic tools. This will certainly add to settle mites as a model group for experimental evolution studies.

In this article, we first review and categorize the studies that have been conducted on experimental evolution of mites. We then analyze the advantages of this group relative to other groups also used in these studies. Finally, we highlight which future directions we believe to be relevant in this field.

EXPERIMENTAL EVOLUTION STUDIES USING MITES

We have surveyed Web of Science using "experimental evolution" and "mite", "artificial selection" and "mite", "laboratory natural selection" and "mite" and "evolution" "selection" and "mite" as keywords. This yielded a total of 16 studies that have used experimental evolution as a methodology and mites as the study organism. Through the search of references cited by these articles and where these articles have been cited, we found an additional 27 studies that matched our query, and an additional reference was pointed out by one referee. This yielded a total of 44 studies on experimental evolution using mites as a model species, which can be categorized according to the characters they study, namely: (1) host plant use, (2) pesticide resistance, (3) behavioral traits, and (4) sex-related traits (sex ratio, sexual dimorphism, sexual selection and its

consequences). We explore these categories separately.

Studies on the evolution of host plant use

Several mite species are herbivorous (Helle and Sabelis, 1985). This group has been particularly studied because of its economic implications, as several species are major pests of economically-relevant crops. The characteristics that make mites excellent models for evolutionary studies are also those that underlie their importance as major crop pests: short generation times and high population growth rates (Sabelis, 1985). Several studies using molecular markers and/or reciprocal transplant experiments in natural populations have shown that mite populations are locally adapted to the host plant they colonize (Magalhães *et al.*, 2007b). This testifies of the strong selection pressure that plants exert upon their mite inhabitants as well of the presence of genetic variation in mite populations to adapt to different host plants. Hence, adaptation of mites to host plants is a process easily amenable to experimental evolution. However, these studies are still scarce (only four) and all of them concern the two-spotted spider mite, *T. urticae*.

The main characteristics and outcomes of these studies are summarized in Table 1. In all cases, adaptation occurred within 17 generations. This indicates that genetic variation for host plant use was high in all initial populations. The fastest response was recorded in a study of adaptation of mites to cucumber (Agrawal, 2000), in which the growth rate of populations selected on cucumber were three-fold higher on that host plant than that of control

lines after five generations of selection only. This study is also the only one in which the base population was collected on four different host plants (instead of one) and maintained in the lab for a very short time before initiating the selection process (cf. Table1). This suggests that populations stemming from several host plants harbour higher genetic variation than populations collected on a single host plant. Developmental time did not evolve in the two studies in which this trait was measured, whereas juvenile survival and fecundity evolved in all four studies, suggesting that genetic variation differs among traits. This suggestion was confirmed in another study (Magalhães *et al.*, 2007a), where it was shown that genetic variation for developmental time was indeed absent. The latter study also showed a lack of response in longevity, despite the presence of genetic variation for this trait, indicating no selection pressure on this trait.

These studies have also shown that adaptation to the host plant used entailed no cost on the ancestral host or on other hosts (Agrawal, 2000; Fry, 1990). Two studies (Gould, 1979; Magalhães *et al.*, 2009) found even positively-correlated responses on some hosts. This may account for the wide host range of *T. urticae* (Navajas, 1998). However, the occurrence of host races (Magalhães *et al.*, 2007b) still awaits an evolutionary explanation.

Studies on the evolution of resistance to pesticides

Because many mite species are pests of several crops, they are often subject to chemical control.

TABLE 1: Characteristics and outcomes of the experimental evolution studies on host plant use in *T. urticae*. EE: experimental evolution; JS: Juvenile survival; Fec: fecundity; devT: developmental time; Long: longevity.

Number collected	Plants of collection	Plants of maintenance	Generations before EE	Plants used in EE	Traits measured	Generation of response	Generations in total	References
200	peach	bean	16	cucumber	JS, fec, devT*	5-15	40	Gould 1979
1000	corn	bean	4	tomato	JS, Fec	10-17	45	Fry 1990
Several hundreds	cotton, bean, roses, morning glories	cotton	4	cucumber	growth rate (JS + Fec)	<5	20	Agrawal 2000
Several hundreds	cucumber	cucumber	400	tomato, pepper	JS, devT*, Fec, Long*	<15	25	Magalhães <i>et al.</i> 2007, 2009

Mite species	Pesticide	Generation before EE	Resistant/Susceptible ratio at LC50	Cross resistance	Genetics	Effects on other traits	Selection pressure	References
<i>Tetranychus urticae</i>	Bifenxtrin	7 field seasons	109		Incompletely dominant			Herron <i>et al.</i> , 2001
<i>Tetranychus urticae</i>	Tebuempyrad	5 field seasons	64.5					Devine <i>et al.</i> , 2001
<i>Tetranychus urticae</i>	Clofentezine		770	10A, 21A, 12B, 1B, 3A (+)				Nauen <i>et al.</i> , 2001
<i>Tetranychus urticae</i>	Hexythiazox		1000		Monogenic dominant			Uesugi <i>et al.</i> , 2002
<i>Tetranychus urticae</i>	Chlofenapyr	5	483		Monogenic dominant completely recessive			Uesugi <i>et al.</i> , 2002
<i>Tetranychus urticae</i>	Etoxazole		>100000					
<i>Tetranychus urticae</i>	Chlofenapyr	3	30.9					Herron and Rophail, 2003
<i>Tetranychus urticae</i>	Spirodiclofen	37	13		Polygenic, incomplete		25% surviving	Rauch and Nauen, 2003
<i>Tetranychus urticae</i>	Chlofenapyr	12	580	19, 1B, 10A (+)			6% surviving	van Leeuwen <i>et al.</i> , 2004
<i>Tetranychus urticae</i>	Fenpyroximate	20	252	21A, 3A, 12C, 6, 21A+3A, UN (+)			50-70% surviving	Kim <i>et al.</i> , 2004
<i>Tetranychus urticae</i>	Fenpyroximate	5	2910	5 (+)	Monogenic incompletely dominant		50 females, 30-50% surviving	Sato <i>et al.</i> , 2004
<i>Tetranychus urticae</i>	Abamectin	5	342	6 (+)				Sato <i>et al.</i> 2005
<i>Tetranychus urticae</i>	Chlofenapyr	6	571				1500 mites, 20-40% surviving	Sato <i>et al.</i> , 2007
<i>Tetranychus urticae</i>	Bifenazate				Mitochondrial control	Growth rate*	10% surviving	van Leeuwen <i>et al.</i> , 2008
<i>Tetranychus urticae</i>	Hexythiazox				Polygenic			
<i>Tetranychus urticae</i>	Etoxazole				Monogenic			
<i>Tetranychus urticae</i>	Spirodiclofen		274	23 (+) 21A, 10B, 20B, UN (-)	Polygenic		5000 larvae, 10-20% surviving	van Pottelberge <i>et al.</i> , 2009b
<i>Tetranychus urticae</i>	Abamectin	15		1B, 12C, 10A, 21A (+)	Incompletely dominant			Yorulmaz and Ay, 2009
<i>Tetranychus urticae</i>	Milbemectin	6	409	6 (+)			1400 mites, 30-40% surviving	Nicastro <i>et al.</i> , 2010
<i>Tetranychus cinnabarinus</i>	Methrin	16	25.8, 3.7, 1.3, 4.0, 2.5					Lin <i>et al.</i> , 2003
<i>Tetranychus cinnabarinus</i>	Abamectin							Lin <i>et al.</i> , 2003
<i>Tetranychus cinnabarinus</i>	Pyridaben							Lin <i>et al.</i> , 2003
<i>Tetranychus cinnabarinus</i>	Dicofol	16 (six months)	100.7			Growth rate (-)		Daghl and Tunc, 2001
<i>Panonychus citri</i>	Hexythiazox	17 field	1000					Yamamoto <i>et al.</i> , 1995
<i>Panonychus ulmi</i>	Hexythiazox	25-30	> 2000	10A, 12B (+)		Fec (+), devT (-)		Pree <i>et al.</i> , 2002
<i>Panonychus ulmi</i>	Clofentezine			negative with 12C, 21A and UN				
<i>Panonychus ulmi</i>	Fenbutatin oxide			10A (-)				Pree <i>et al.</i> , 2002
<i>Brevipalpus phoenicis</i>	Hexythiazox	2	>10000					Campos and Onoto, 2002
* No response observed								

TABLE 2: Characteristics and outcomes of experimental evolution studies on the evolution of resistance to pesticides in herbivore mites. EE: experimental evolution; JS: Juvenile survival; Fec: fecundity; devT: developmental time; Long: longevity. Empty cells: not applicable.

The repeated use of pesticides has inadvertently provided a field experiment of evolution, as pesticides pose a strong selection pressure on populations, possibly resulting in the evolution of resistance. Indeed, if some individuals of a population treated with a pesticide are able to survive and this ability is genetically determined, the frequency of resistant individuals in the population will increase, hence resistance will evolve. The urge to prevent or solve the ineffectiveness of pesticides due to the evolution of resistance in mites has promoted research on this subject.

Most literature on resistance to pesticides in mites concerns studies of toxicity that compare mortality induced by pesticides among mite populations from treated and untreated orchards. Here we review only the studies involving artificial selection, where the experimenter exerts a selection pressure (repeated pesticide treatment) on mite strains and compares their survival after treatment with that of unselected mite strains. In most studies, the selected character is survival after treatment, in which only mites surviving the pesticide treatment contribute to the next generation. However, other traits, such as fecundity, can also be affected by pesticides and could potentially be used in these studies (Van Pottelberge *et al.*, 2009a). Some studies involve selection for susceptibility to pesticides, instead of resistance. In these studies, the selected character is mortality after treatment: mites are allowed to reproduce before the pesticide treatment, and only the progeny of susceptible mites (i.e. non-surviving mites) contributes to the next generation (Nicastro *et al.*, 2010; Sato *et al.*, 2005; Sato *et al.*, 2004; Sato *et al.*, 2000; Sato *et al.*, 2007; Sato *et al.*, 2006; Yamamoto *et al.*, 1996). In addition, some studies address the evolution of resistance in predatory mites that are used as biological control agents of crop pests. In this case, resistance is a desired trait. Indeed, if pesticide resistance evolves in predatory mites that are used as biocontrol agents, these can be introduced in combination with pesticides.

We review 30 studies where artificial selection is applied on mite populations (cf. Tables 2 and 3). From these, 22 focus on herbivorous mites, of which 16 focus on *T. urticae* and the remaining con-

cern *Panonychus ulmi*, *Panonychus citri*, *T. cinnabarinus* and *Brevipalpus phoenicis* (vector of *Citrus leprosis virus*). Eight studies focus on the evolution of resistance in predatory mites, namely in *Amblyseius womersleyi*, *Amblyseius fallacis*, *Typhlodromus pyri*, *Phytoseiulus persimilis* and *Amblyseius cydnodactylon*.

In these studies, artificial selection was applied during several generations, ranging from three generations (Campos and Omoto, 2002) to seven field seasons (Herron *et al.*, 2001). However, in several studies the number of generations that the selection process lasted is not indicated (cf. Tables 2 and 3). After selection, the resistance ratio is usually calculated as the LC50 from selected strains divided by that of control strains, LC50 being the dose required to kill 50% of the population under study after a specific time. In the studies reviewed here, the resistance ratio obtained ranged from four (Solomon and Fitzgerald, 1993) to more than 100000 (Uesugi *et al.*, 2002). The duration of the selection process did not affect the resistance ratio.

Selection pressures ranged from 6% (Van Leeuwen *et al.*, 2004) to 50-70% (Kim *et al.*, 2004) of mites that contribute to the next generation. Higher selection pressures did not result in faster evolution of pesticide resistance. However, several studies did not mention the selection pressures or the number of individuals used per treatment to maintain the selected mite strains. We found only one study in which resistance to pesticides did not evolve: after 12 months of selection with Fenvalerate, the predatory mite *Phytoseiulus persimilis* did not show an increase in survival after treatment (Markwick, 1986).

In addition to the description of the selection process, some studies also addressed: a) the genetic basis of pesticide resistance, b) the mechanism of resistance, c) fitness costs associated to resistance to pesticides, and/or d) cross resistance with other pesticides with the same or a different mode of action. In Tables 2 and 3 we summarize these results. None of the studies reviewed include all topics referred, although some include nearly all (Pree *et al.*, 2002; Sato *et al.*, 2004; Van Leeuwen *et al.*, 2004; Van Pottelberge *et al.*, 2009b).

a) One major goal of studies on the evolution of

resistance to pesticides is to unravel the genetics of resistance (number of genes involved, dominance, etc). To this aim, reciprocal crosses between resistant and susceptible strains (F1), then either F1 X F1 crosses (F2) and/or F1 X parental line crosses (backcrosses) are done, and mortality due to pesticides is measured.

Eighth of the studies reviewed here dealt with the genetics of resistance. All of them found a Mendelian inheritance mode except one, where inheritance of resistance to Bifenazate in *T. urticae* was found to be exclusively under mitochondrial control (Van Leeuwen *et al.*, 2008). In the remaining studies, the dominance of the pesticide resistance trait ranged from completely recessive to completely dominant (Tables 2 and 3). Pesticide resistance was found to be monogenic in three cases, and controlled by more than one gene in four cases. Unfortunately, the latter studies did not fur-

ther test how many genes were involved in determining pesticide resistance. Another concern is that the same characteristic (resistance to Chlorfenapyr) in the same mite species (*T. urticae*) yielded different results in two different studies (monogenic and completely recessive in one study (Uesugi *et al.*, 2002) and polygenic and incomplete recessive in the other (Asahara *et al.*, 2008). Hence the results found could well be population, rather than species specific.

b) The potential mechanisms of resistance were investigated in eight studies by applying synergists together with the pesticides. Synergists block a specific enzyme. If resistance is reduced upon application of the synergist, this means that the metabolic pathway inhibited by the synergist confers resistance to the pesticide under study. Artificial selection lines are particularly useful to these studies, as they are expected to differ from control lines in the

TABLE 3: Characteristics and outcomes of the experimental evolution studies on evolution of resistance to pesticides in predatory mites. R/S ratio: resistant/susceptible ratio. Symbols are as in Table 2.

Mite species	Pesticide	Generations before EE	R/S ratio at LC50	Cross resistance	Genetics	Effects on other traits	Selection pressure	References
<i>Amblyseius fallacis</i>	Permethrin	12	64	1B				Strickler and Croft, 1982
<i>Amblyseius fallacis</i>	Permethrin + Azinphosmethyl							
<i>Amblyseius fallacis</i>	Permethrin							
<i>Amblyseius womersleyi</i>	Permethrin	10						Mochizuki, 1997
<i>Amblyseius womersleyi</i>	Methidathion	4	342	1B			850 mites, 35-44% surviving	Sato <i>et al.</i> , 2000
<i>Amblyseius womersleyi</i>	Methidathion		153-287				1500 females, 20-40% surviving	Sato <i>et al.</i> , 2006
<i>Amblyseius cydnodactylon</i>	Malathion	16	54			Fecundity (-)		El-Banhawy <i>et al.</i> , 2000
<i>Typhlodromus pyri</i>	Mancozeb	10	73		Monogenic codominant			Auger <i>et al.</i> , 2005
<i>Typhlodromus pyri</i>	Deltamethrin	14 appl.	4					Solomon and Fitzgerald, 1993
<i>Typhlodromus pyri</i>	Cypermethrin	6	10	6				Markwick, 1986
<i>Phytoseiulus persimilis</i>	Fenvalerate	12 months	no response					
<i>Phytoseiulus persimilis</i>	Organophosphorus pesticides					devT*, growth rate*, predation rate (+)		Atanassov, 1997

pesticide resistance trait only, and not in other characteristics. These studies have been done in *T. urticae* (Kim *et al.*, 2004; Rauch and Nauen, 2002; Van Leeuwen *et al.*, 2004; Van Leeuwen *et al.*, 2008; Van Pottelberge *et al.*, 2009c; Yorulmaz and Ay, 2009), *Panonychus ulmi* (Pree *et al.* 2002), and in the predatory mite *Amblyseius womersleyi* (Sato *et al.*, 2006). In one case the mechanism of resistance in *P. ulmi* was not found (Pree *et al.*, 2002). The most frequent mechanisms of resistance found were the activities of cytochrome P450 monooxygenase and esterases.

c) Fitness costs associated to the evolution of resistance were explored in five studies, by measuring the developmental or reproductive traits of selected mite strains as compared to unselected strains. Fitness costs associated with the evolution of resistance to pesticides were found in *Panonychus citri*, *Panonychus ulmi* and in the predatory mite *Amblyseius cydnodactylon* (El-Banhawy *et al.*, 2000; Pree *et al.*, 2002; Yamamoto *et al.*, 1995b). No effects on fitness were found in *Phytoseiulus persimilis* and in *T. urticae* (Atanassov, 1997; Van Leeuwen *et al.*, 2008). In two other studies, the fitness costs of resistance from strains selected in the laboratory in a different study were measured (Franco *et al.*, 2007; Van Pottelberge *et al.*, 2009a). These studies found no fitness costs associated to evolution of resistance in *Brevipalpus phoenicis* and in *T. urticae*, respectively. Ten studies addressed the persistence of the resistance trait once pesticides were removed. In most cases, resistance was quickly lost after few generations in pesticide-free environments (Dagli and Tunc, 2004; Nicastro *et al.*, 2010; Pree *et al.*, 2002; Rauch and Nauen, 2002; Sato *et al.*, 2005; Sato *et al.*, 2004; Van Pottelberge *et al.*, 2009c; Yamamoto *et al.*, 1996). This suggests that fitness costs were associated to resistance to pesticides, otherwise resistance was expected to be maintained in the population. The only exception was a study on resistance to Hexithiazox in *Brevipalpus phoenicis*, in which resistance was maintained throughout the seven months that the study lasted (Campos and Omoto, 2002). Pree *et al.* (2002) found that resistance to Clofentezin was lost after three generations in a mixed population, but in a resistant population it lasted at least 10 generations and field observations sug-

gested that it lasted for two field seasons. In another study, resistance to Permethrin in *Amblyseius womersleyi* was stable during 20 months, and it was subsequently lost (Mochizuki, 1997), suggesting that, given enough time, susceptibility may be recovered. Altogether, these studies suggest that the evolution of pesticide resistance in mites entails costs in most, but not all, cases.

d) In 12 of the studies reviewed here, cross-resistance was explored with pesticides from the same and/or different mode of action (Tables 2-4). In almost all of them cross resistance was found. However, its occurrence does not seem to be related to the similarity between the mode of action of the pesticides tested.

In summary, studies on evolution of resistance have shown a rapid evolution of pesticide resistance, often entailing fitness costs in pesticide-free environments. Cross-resistance with other pesticides was found in most cases, independently of the mode of action of each pesticide. The genetic basis of pesticide resistance was found to be extremely variable across studies, even those involving the same pesticide and the same species. In contrast, the enzymes coded by those genes that confer resistance seem to be more invariable, although the paucity of studies on this topic hampers general conclusions.

Studies on the evolution of behavioral traits

A behavioral trait can be defined as any observable reaction or movement made by an organism in response to external or internal stimuli. Studies on the evolution of behavioral traits using mites have considered traits that enable mites to deal with harsh environmental conditions. Specifically, these studies have addressed the evolution of a) diapause, and b) dispersal in tetranychid mites. In addition, one study has addressed the evolution of several foraging traits in *Phytoseiulus persimilis*.

Diapause

Diapause is a period in which individual growth or development is suspended and physiological activity is diminished in response to adverse environmental conditions. It occurs in many mite

species. Four studies have performed artificial selection with this trait (Table 5). In all studies, a response was obtained after a maximum of seven generations, both for higher and lower diapause capacity (*i.e.*, percentage of diapausing individuals in the populations under study). These studies also addressed the genetic basis of this trait and the effect of selection on other traits.

Two studies subjected populations to artificial selection to unravel the genetic basis of diapause

(Kawakami *et al.*, 2010; So and Takafuji, 1992). So and Takafuji (1992) created five high diapause (HD) and five low diapause (LD) lines, each starting from a different base population (Table 5). Line crosses, performed with three out of these five populations, suggested that dominance varied with the population under study: in one population the trait was mostly additive whereas in two others the low diapause phenotype seemed to be dominant. Kawakami *et al.* (2010) selected a non-diapausing

TABLE 4: Mode of action of pesticides used in the studies on evolution of resistance in herbivore and predatory mites. Group: Group of mode of action according to IRAC (Insecticide Resistance Action Committee) (IRAC, 2009).

Pesticide	Mode of action	Group
Acephate	Acetylcholinesterase inhibitors	1B
Azinphosmethyl	Acetylcholinesterase inhibitors	1B
Chlorpyrifos	Acetylcholinesterase inhibitors	1B
Dimethoate	Acetylcholinesterase inhibitors	1B
Malathion	Acetylcholinesterase inhibitors	1B
Methidathion	Acetylcholinesterase inhibitors	1B
Organophosphorous	Acetylcholinesterase inhibitors	1B
Acrinathrin	Sodium channel modulators	3A
Bifenthrin	Sodium channel modulators	3A
Cypermethrin	Sodium channel modulators	3A
Deltamethrin	Sodium channel modulators	3A
Fenpropathrin	Sodium channel modulators	3A
Fenvalerate	Sodium channel modulators	3A
Permethrin	Sodium channel modulators	3A
Abamectin	Chloride Channel activator	6
Milbemectin	Chloride Channel activator	6
Clofentezine	Mite growth inhibitors	10A
Hexythiazox	Mite growth inhibitors	10A
Etoxazole	Mite growth inhibitors	10B
Azocyclotin	Inhibitors of mitochondrial ATP synthase	12B
Cyhexatin	Inhibitors of mitochondrial ATP synthase	12B
Fenbutatin oxide	Inhibitors of mitochondrial ATP synthase	12B
Propargite	Inhibitors of mitochondrial ATP synthase	12C
Chlorfenapyr	Uncouplers of oxidative phosphorylation via disruption of the proton gradient	13
Amitraz	Octopamine receptor agonists	19
Acequinocyl	Mitochondrial complex III electron transport inhibitors	20B
Fenpyroximate	Mitochondrial complex I electron transport inhibitors	21A
Pyridaben	Mitochondrial complex I electron transport inhibitors	21A
Tebufenpyrad	Mitochondrial complex I electron transport inhibitors	21A
Spirodiclofen	Inhibitors of acetyl CoA carboxylase	23
Spiromesifen	Inhibitors of acetyl CoA carboxylase	23
Dicofol	Unknown mode of action	UN

strain starting from a diapausing population, by collecting individuals that did not diapause when the population was subjected to diapause-inducing conditions. A decrease in diapause incidence was found after the first generation. Subsequently, the authors crossed the base population with the low-diapause line obtained and with two other populations where diapause incidence was low. Crosses with the low-diapausing line yielded a recessive non-diapausing phenotype, whereas this phenotype was completely dominant in crosses with the two wild-derived populations. Moreover, the genetic basis of dominance was probably different in these two non-diapausing populations.

In two other studies, the consequences of the selection process for other life-history traits were tested (Ito, 2009; So and Takafuji, 1991). So and Takafuji (1991) measured six life-history traits (embryonic developmental time and egg to adult development time, age at first oviposition, fecundity and longevity of females, and sex ratio) of two differ-

ent populations of *T. urticae*, at four different temperatures. They found a positive genetic correlation between diapause incidence and embryonic developmental time, egg to adult developmental time, and fecundity at high temperatures (Table 5). Recently, Ito (2009) found no evidence for a genetic correlation between diapause and fecundity or developmental time in *T. kanzawai* (Table 5), suggesting that in this species these traits may evolve independently.

Dispersal

Several mite species live in environments that vary in quality with time, either due to extrinsic factors, such as seasonality, or to intrinsic factors, such as increased competition due to population growth at a local scale. Moreover, the resources they consume are often patchily distributed. Therefore, dispersal is an extremely relevant trait in the ecology of these species (Kennedy and Smitley, 1985; Sabelis and Dicke, 1985). Yet, only three studies have addressed

TABLE 5: Characteristics and outcomes of the experimental evolution studies on behavioral traits. SR: sex ratio, Ovip Rate: Oviposition rate. Other symbols are as in Table 1.

Selection trait	Mite species	Number of mites per population	Time before experiments	Effects on other traits	Generation of response	Total generations	References
High and low diapause	<i>Tetranychus urticae</i>	100	0		1-7	15	So and Takafuji, 1992
High and low diapause	<i>Tetranychus urticae</i>	100 or 50	> 20 generations		2	2	Kawakami <i>et al.</i> , 2010
High and low diapause	<i>Tetranychus kanzawai</i>	89	5 months	Fec*, devT*	5	14	Ito, 2009
High and low diapause	<i>Tetranychus urticae</i>	> 100	Not mentioned	devT (+), Fec (+), Long,* SR*	1-3	15	So and Takafuji, 1991
High and Low dispersal	<i>Oligonychus pratensis</i>	300-500	3 months		> 4	9	Margolies, 1993
High and Low dispersal	<i>Tetranychus urticae</i>	100	18 months (30 Generations)	Fec*, SR*	> 1	8	Li and Margolies, 1994
High and Low dispersal	<i>Tetranychus urticae</i>		40 Generations	SR*, Ovip rate (-)	5	5	Yano and Takafuji, 2002
Consumption rate	<i>Phytoseiulus persimilis</i>	200-350		Consumption -> conversion (-)	1-6	10-12	Nachappa <i>et al.</i> , 2010
Conversion rate				Dispersal -> olfactory response (+)			
Dispersal				Consumption -> dev (+)			
Olfactory response				Consumption -> fec (+) Conversion -> fec (+)			

* No response observed

the evolution of dispersal using mites. In these studies, a response to selection occurred within a maximum of five generations.

One study used bi-directional artificial selection to measure intra-specific genetic variation in dispersal behaviour of the bank grass mite, *Oligonychus pratensis* (Margolies, 1993). Two other studies performed bi-directional artificial selection of populations of the two spotted spider mite *T. urticae* (Li and Margolies, 1994; Yano and Takafuji, 2002). Li and Margolies (1994) tested whether aerial dispersal in *T. urticae* was correlated with two life-history traits that are associated with colonization of a new habitat, i.e., fecundity and sex-ratio. They found that fecundity and sex-ratio were not genetically correlated to dispersal ability (Table 5). On the other hand, Yano and Takafuji (2002) found a negative genetic correlation between oviposition rate and dispersal capacity, but only when the two artificially selected strains were tested on plants of low quality (Table 5). When tested plants were of high quality no differences in oviposition rates were observed between strains. In agreement with Li and Margolies (1994), they found no correlation between dispersal and sex-ratio (Table 5).

Foraging

In a recent study, Nachappa and colleagues performed artificial selection with several foraging traits of the predatory mite *P. persimilis* when feeding on its prey *T. urticae*, namely consumption and conversion rates, dispersal and olfactory response to prey volatiles (Nachappa *et al.*, 2010). They obtained a response to all traits within 2-7 generations. Correlations among these traits and with life-history traits (fecundity, survival, developmental rate and intrinsic growth rate) were either positive or absent, except for consumption and conversion rates, where a negative correlation was observed (Table 5).

In summary, eight studies used artificial selection experiments to study the evolution of behavioral traits. In all of them, mite populations responded to artificial selection after very few generations. The genetic basis of these traits, as well as cor-

relations with other traits, varied with the species and the population under study.

Studies on sex-related traits

In this category, we group one study on the evolution of sex ratio (Okabe and Oconnor, 2003) and a series of studies on sexual selection and its consequences in the bulb mite *Rhizoglyphus robini* by Radwan and colleagues (Jarzebowska and Radwan, 2010; Konior *et al.*, 2006; Radwan, 1998; 2003; Radwan *et al.*, 2004; Tilszer *et al.*, 2006). Other studies on sex-related traits were done by this team but without using the methodology of experimental evolution.

The study on sex ratio was done using artificial selection on a population of *Schwiebia elongata*, starting from a single female and with one replicate line only (Okabe and Oconnor, 2003). No details on the original base population were provided. They showed that male frequency increased from 0 to 30% within five generations. Hence, sex ratio is a genetically-determined trait with high genetic variance in this mite. In another study using isofemale lines in *T. urticae*, sex ratio was also found to be a heritable trait (Vala *et al.*, 2003).

Radwan and colleagues used a population of *R. robini* collected in a single location and initiated with around 200 individuals to perform a series of elegant experiments on sexual selection. The first experiments were done 2-3 months after the population was brought to the lab (4-6 generations), the latest after 100 generations. In a first study (Radwan, 1998), artificial selection for sperm competition was performed. The authors used 100 males in each selection line ($N = 3$), of which the 25 ones that produced a more competitive sperm were able to mate with a female to form the next generation. After four generations of selection, they found increased sperm competitiveness in all selection lines relative to the controls.

In *R. robini*, males can either be homeomorphic (with unmodified legs) or heteromorphic (with a thickened third pair of legs, used to puncture the cuticle of other males in fights). Radwan (2003) let 50 females choose between homeomorphic or heteromorphic males during 8-10 generations. At

each generation, females that had mated with a homeomorphic male were allocated to one selection regime, females that had mated with a heteromorphic male to another (two replicate lines per treatment). In the following generation, the female offspring emerging from those females was again let to choose between the two male types, and the same procedure was repeated. The proportion of each morph was then measured and heritability calculated. He found asymmetric heritability: 0.3 in lines where females chose heteromorphic males, 0.8 in lines where females chose homeomorphic males. This asymmetry was attributed to dominance of the homeomorphic male. However, several other factors, such as drift, inbreeding depression, indirect selection, and genes of large effect, may have contributed to this asymmetry (Falconer, 1989).

Next, a study was performed to analyse the evolution of male-female interactions (Tilszer *et al.*, 2006). Mites were let to evolve during 37 generations under two selection regimes (three lines per regime): in the first, each female was offered one male only to mate with (monogamous lines), whereas in the second five females were interacting with five males during mating (polygamous lines). At the end of the selection period, the reproductive success of males and females from each selection regime was tested when interacting with the opposite sex, stemming from each selection regime. Each line was composed of 100 females and only heteromorphic males were used. They found that females from monogamous lines had reduced reproductive success when interacting with males from polygamous lines. This is probably because in monogamous lines the interests of males and females are aligned, whereas this is not the case in polygamous lines. Females from polygamous lines did not show this decrease in reproductive success when exposed to males from those lines, probably because they have coevolved a defence mechanism. Other traits (survival, male reproductive success and inbreeding depression) were not affected by the selection process.

Finally, two studies were performed to unravel the effects of sexual selection in purging deleterious mutations. In the first one (Radwan *et al.*,

2004) three selection regimes, each replicated three times, were created: 1- one female was offered one randomly-selected male, 2- five females were let to mate with five males, and 3- the whole selection line was not subdivided. Each line was composed of 60 females in total. The expectation was that fitness would be reduced in the selection regimes with subdivided populations (1 and 2), due to the accumulation of deleterious mutations, but that this effect would be partially rescued in the regime where sexual selection could be expressed (2). After 11 generations, fecundity was lower in regimes 1 and 2 as compared to 3, but no difference was found between regimes 1 and 2. Survival, longevity and the frequency of each male morph did not change. It can be concluded that mutation accumulation occurred, but sexual selection could not counter it.

In a subsequent study (Jarzebowska and Radwan, 2010), the same set-up was used except that each population was composed of five females only. Under the Monogamous selection regime (M), females mated with one male each, whereas under the Sexual Selection regime (SS), the five females were let to mate with the five males. There were 50 replicate lines per selection regime and the response was measured after eight generations of selection. The authors found that the number of lines that went extinct (presumably due to the accumulation of deleterious mutations) was lower in the SS than in the M regime. Inbreeding depression was also reduced in the SS regime. These results show that sexual selection can indeed counter the effects of inbreeding depression in small populations.

DISCUSSION

Overall, studies of experimental evolution using mites have yielded fast responses of all traits under scrutiny. Indeed, most responses occurred within the first 10 generations of selection, with a maximum of 37 generations. Traits measured were not morphological but rather behavioral or ecological. As these traits are expected to respond slower than morphological traits (Houle, 1992), we can speculate that morphological traits in these species would respond at an even faster pace. Most correlated

responses were absent, suggesting that traits can evolve independently. Of the correlated responses that were significant, most of them were positive. Hence, correlated responses are not expected to hamper significantly responses to selection in mites.

High genetic variance

The results of the studies gathered in this review indicate that the populations under study harboured high genetic variation for the traits under scrutiny. Several factors may contribute to this. First, some of the populations from which lines were selected have been collected from several host plants. This may contribute to a high genetic variance of the mite population, as different hosts impose different selection pressures upon populations. Another possibility is that most populations have been in the laboratory for a short time before the experiments were done. This procedure may contribute to a higher genetic variance for the traits tested in two ways. First, if traits are counter-selected in the laboratory (*e.g.* dispersal), then alleles for high dispersal may be lost when populations remain for long periods in the laboratory. Second, because laboratory populations are usually composed of fewer individuals than field populations, alleles in the laboratory are more prone to be lost due to drift. Hence, tests performed on recently wild-derived populations may lead to faster responses than studies on laboratory populations. However, some of the studies reported here were done on populations collected from a single host (Magalhães *et al.*, 2009; Magalhães *et al.*, 2007a; So and Takafuji, 1992; Yano and Takafuji, 2002) and/or on populations that had been for a long time in the laboratory (Jarzebowska and Radwan, 2010; Magalhães *et al.*, 2009; Magalhães *et al.*, 2007a; Tilszer *et al.*, 2006) and yet responses were still rapid. To test whether these effects are indeed relevant, one should compare the genetic variance of populations collected from a single or multiple plants, and with variable time in the laboratory.

Another factor that may contribute to high genetic variance is that most traits under selection may not be advantageous in all environments, hence it is expected that some genetic variance remains in the populations. A typical example of this

is dispersal, which is advantageous when resources are locally scarce but globally abundant, but should be selected against otherwise. Indeed, dispersing entails costs, as individuals may end up in a patch even more adverse than the current one. This is particularly true in mites, for which dispersal is mostly passive. The same is true for diapause, which is favourable only when conditions are adverse. Pesticide resistance is also a trait that is usually beneficial when populations are exposed to the pesticide but deleterious otherwise (Coustau *et al.*, 2000), but see (Lopes *et al.*, 2008; McCart *et al.*, 2005). Hence, it is also a trait susceptible to harbour high genetic variance. Host-plant use is more puzzling, as high performance on one host seems to have no consequences on other hosts, or it entails a positive correlation with performance on other hosts. Thus, factors other than negative genetic correlations across environments need to be invoked to account for the high genetic variance of these traits. It may well be that different sets of genes underlie adaptation to different host plants, even though no negative correlation between them occurs. As mites face different host plants at different times, this may be sufficient to maintain genetic variance. Another possibility is that adaptation to host plants trades off with resistance to pathogens or predators.

Genetic basis of phenotypes

Whenever specific tests were done to address the genetic basis of the traits studied, a simple genetic basis was inferred in many cases. This may also contribute to the fast responses observed. Moreover, because few genes seem to be involved in the response, the role of recombination in increasing the speed of the response is reduced. In this case, the mating system of most mites under study (*i.e.* haplodiploidy) is expected to increase the speed of the response, as compared to diploid organisms (Hall, 2000). This is particularly relevant when phenotypes are recessive, as in that case they are still expressed in the male population of the haplodiploid species.

Several authors have suggested that monogenic resistance to pesticides is favoured under field conditions (Carriere and Roff, 1995; McKenzie *et al.*,

1992; Roush and McKenzie, 1987). Indeed, acaricide resistance is mainly under monogenic control (Goka *et al.*, 1998; Herron and Rophail, 1993; Martinson *et al.*, 1991; Yamamoto *et al.*, 1995a), although there are some examples of polygenic control (Clark *et al.*, 1995; Keena and Granett, 1990; Mizutani *et al.*, 1988). However, resistance to the same acaricide may be controlled by one or multiple loci in different populations (Asahara *et al.*, 2008). Hence, the genetic basis of pesticide resistance is not necessarily related to the mode of action of pesticides. Possibly, the selection process itself may constrain the genetic basis of the phenotypes obtained. Indeed, strong selection pressures may contribute to obtaining phenotypes with a simple genetic basis, whereas weaker selection pressures allow for more complex genetic bases (Ffrench-Constant *et al.*, 2004). Therefore, studies on the evolution of resistance to pesticides will benefit from exploring the past selection history of a population to predict evolutionary outcomes.

Ecological relevance of the traits under study

A particularly relevant feature of mites is the fact that their ecology is widely studied. This is reflected in the ecological significance of the traits measured. Moreover, some traits have an economic importance. Indeed, the first two sections concern the fact that mites are major crop pests. This prompted the research on host plant use, because knowledge on the evolutionary consequences of feeding on a particular host can provide tools for an appropriate pest management programme. The evolution of acaricide resistance being a major concern for crop breeders, research on this issue provides valuable information. Artificial selection on the foraging traits of *P. persimilis* is also prompted by the fact that this predatory mite is an efficient biocontrol agent of a major crop pest, *T. urticae*. Dispersal and diapause are two major adaptations to changing environments. Indeed, most mites occur in unstable environments, such as seasonal crop plants. Hence, dispersal and diapause provide a means to face adverse environmental conditions. The studies of sexual selection were motivated by specific features of *Rhizoglyphus robini*, in particular the occurrence of

heteromorphs in males.

These studies thus underscore the added value of using mites for experimental evolution studies. Indeed, not only are they good models because a response to selection can be obtained within few generations, but also several ecologically-relevant traits are amenable to this kind of experimentation. This feature is in sharp contrast with the traditional model organisms for experimental evolution, namely *D. melanogaster* and *Escherichia coli*. Indeed, the study of the ecology of these species lags behind, hence most experimental evolution studies performed on these species aim at testing features that are not directly relevant to the species under study.

Future perspectives

Although the results stemming from the studies reviewed here were extremely relevant, the interpretation of some of them was hampered by the lack of information provided. Indeed, sometimes the number of generations or the number of individuals involved in the selection process were not mentioned. In those cases, it is not possible to infer the speed of the response and the strength of selection, respectively. In a few cases, no replicate lines were used, hence it is difficult to know whether the response observed is a general phenomenon or not. It would be useful to fill these caveats in future studies in order to increase the power of mites as model systems for experimental evolution.

Even though all studies on experimental evolution in this group are grounded upon a wide knowledge of their ecology, we believe that several features are still under-explored. Namely, there is a wide variety of studies on ecological interactions in mites, and these could be explored from an evolutionary perspective. In particular, it would be interesting to further investigate the evolution of the interaction between herbivorous mites and their natural enemies used in biological control. Several other traits could be used (antipredator behaviour, cannibalism, etc).

Another major research avenue is being opened by the whole genome sequencing of the spider mite *T. urticae*. This will provide a new tool that can be

used in studies of experimental evolution. For example, the evolution of host-plant use can be addressed not only at the phenotypic level, as it has been so far, but also from a functional genomics perspective, as it is now possible to search for the genomic regions that underlie host-plant adaptation in the populations that are subject to experimental evolution. This genome will not only serve for studies on this mite species, it will also be useful to our understanding of the genetic basis of phenotypes of several other species, as the *T. urticae* genome is the first chelicerate whose genome has completely sequenced (Grbic *et al.*, 2007).

The studies on experimental evolution using mites that have been done so far, together with the future perspectives that are opening to this group proves that mites are an excellent model to perform these studies, hence this field is probably as yet in its infancy.

ACKNOWLEDGEMENTS

The authors would like to thank Margarida Matos for insightful comments on this manuscript.

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