The interplay between genetic and learned components of behavioural traits: olfactory responses of predatory mites to signals contained in a herbivore-induced plant volatile
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This thesis deals with the evolution of behavioural traits that have both a genetic basis and can be modified; the modification I have examined concerns an adaptive (learnt) response to environmental influences. In theory, the evolution of such traits may lead to two extreme outcomes, one where the trait becomes genetically fixed (and phenotypically invariable), and the other where it is entirely shaped by environmental influences. Between these extremes lies a spectrum of traits containing a genetic component but also, to differing degrees, a modifiable component. A recurring question in evolutionary biology is how phenotypic plasticity (i.e., the ability to modify a phenotype in response to external or internal influences) may influence the rate of evolution of a trait that itself has a genetic basis. To address this question we require a model system in which there is (a) a genetic variation for both the genetically determined behavioural trait and the ability to learn, and (b) in which the level of learning and the innate value of the behavioural trait represent separate quantifiable traits. Theoretical predictions may also be obtained by tracking the evolution of such a behavioural trait in a theoretical model system.

The first part of this thesis contains the experimental tests for the presence of genetic variation in the behaviour of the predatory mite, *Phytoseiulus persimilis*, towards specific plant odours. These odours are blends of volatile compounds that plants emit when infested by a herbivorous mite that represents prey to the predatory mite. They are referred to as HIPV, which is shorthand for herbivore-induced plant volatiles. The composition of the blend of volatiles is specific to the combination of plant species and herbivore. Therefore, it has been proposed that natural enemies of the herbivores may use HIPV as signals of prey presence and thereby locate their prey. This hypothesis is supported by the well-documented attraction of predatory mites to HIPV. However, blends of volatiles are known to vary between plant species, and to vary with differing size and duration of infestation. Moreover, in a natural setting different plant species co-occur and may be infested by multiple species of herbivores. This begs the question, how predators extract a signal of prey presence from the variation in the blends of HIPV.
HIPV. Adaptive learning may serve to update and reinforce predator preferences for specific volatiles (or their mixtures) after experiencing these in the presence of suitable prey. Moreover if specific HIPV are consistently coupled with the presence of prey, then genetically determined predator preferences for these HIPV may evolve by natural selection. However, existing evidence for genetically determined responses to HIPV in *P. persimilis* is contradictory. Some studies demonstrate a preference of the predators to a specific HIPV even if they have no prior experience with these plant volatiles. In contrast, other studies report that prior experience with a particular HIPV may be necessary to trigger the preference for that volatile. However these studies measure predator behaviour at the population level, and thus, in genetically variable populations. To date there is little evidence for genotypes differing with respect to preference for a particular HIPV in a natural population, although a genetic basis for the responses of *P. persimilis* to full blends of volatile compounds induced by the prey has been demonstrated.

In part I of this thesis I investigated the genetic basis for the response of *P. persimilis* to a volatile compound induced by the feeding of a herbivorous mite, *Tetranychus urticae*, its prey. Evidence to date indicates that this compound, methyl salicylate (MeSa), is a volatile consistently present in the blend induced by *T. urticae* when feeding on a variety of plant species. In the first two chapters I have presented tests of the genetic basis for the response of *P. persimilis* to MeSa. To this end I have used two approaches: the iso-female line approach (Chapter 2), and purifying selection withing isofemale lines (Chapter 3).

In Chapter 2 I have shown that there is variation in predator responses to MeSa among genetically homogenous lines (the iso-female lines) of the predator, and thus confirming that there is a genetic component in this behaviour. Moreover I have demonstrated that predator responses to MeSa are context-dependent in that they are modified both by the physiological state of the predators (i.e., whether they are well fed or starved), and by the background odours of volatiles released by uninfested plants. These results indicate that this behaviour has evolutionary potential, i.e., it has the ability to respond to selection. Moreover they suggest that the responses of this predator to MeSa may depend on an ecologically relevant context of other volatiles (i.e., volatiles associated with the presence of the prey).

In Chapter 3, I selected within iso-female lines for genotypes with contrasting responses of *P. persimilis* to MeSa offered as a pure compound. The selection was purifying in the sense that two groups of iso-female lines were established and in one group the lines were propagated via females that showed a preference for MeSa, whereas in the second group the lines were propagated via females that avoided MeSa. I hypothesized that the propagation of iso-female lines through individuals that exhibited either preference for MeSa or aversion
to MeSa would lead to a shift in the mean responses of those lines towards, respectively, preference for MeSa or aversion to MeSa. Contrary to these predictions, I observed a shift in the mean response to MeSa in the direction opposite to the selection criterion. At the same time this study confirmed that there is a genetic component in the predator responses to MeSa (reflected in the variation among the genetically homogeneous iso-female lines used in the selection). One possible explanation for this result is a correlation between predator mating preferences and the response to MeSa. In previous studies, more often than not, the focus has been on the response of females to HIPV. Our results caution that in order to understand the evolution of this behaviour, future studies should address the response to HIPV of males as well as females.

Finally, in Chapter 4 I used the iso-female line approach to study whether genetically determined predator responses to MeSa can be modified in response to experience. The ability to learn has been demonstrated for this predator only at the population level. By analysing the responses of different iso-female lines both prior to and after an experience with MeSa, I have demonstrated that there are different genotypes with respect to learning ability. Consequently this predator trait may evolve jointly with the genetically determined preference for MeSa (or other HIPVs).

In the second part of this thesis I explored theoretical predictions for the evolution of behavioural traits modified by adaptive learning, i.e., the learning to improve fitness. In particular, I addressed the hypothesis that adaptive learning accelerates the rate of evolution of a genetically determined trait. This hypothesis is referred to in the literature as the Baldwin effect. Theoretical studies of this effect (reviewed in the Chapter 5) predict that adaptive learning may either accelerate evolution of the genetically determined behaviour or it may slow down the evolution. Adaptive learning changes the rate of evolution by modifying the fitness of different phenotypes. In particular when adaptive learning increases the fitness differences among different phenotypes then the response to selection is stronger, and thus evolution speeds up. In contrast when adaptive learning decreases the fitness differences, then the response to selection is weakened, and evolution slows down. There are two factors that determine how adaptive learning affects the fitness differences among different phenotypes: (a) the shape of the fitness landscape, and (b) the potential of adaptive learning to modify the genetically determined phenotype (i.e., whether the net effect of learning on phenotypic fitness is large or small). These predictions concern the effect of learning on the rate of evolutionary change from one generation to the next. However, allowing learning to evolve causes a change in the long-term dynamics on complex fitness landscapes (such as a rugged landscape) and thus the extrapolation from local evolutionary changes (one generation to the next) to longer time frames is not possible.
To date most studies that have examined the Baldwin effect assumed a fixed (non-evolving) level of learning, and tracked the rate of evolution of the innate (i.e., genetically determined) trait. In Chapter 6 I expanded this theory by tracking the rate of evolution when both the innate trait and the level of learning are allowed to evolve. Comparing these approaches I determined that allowing adaptive learning to evolve greatly reduces the number of generations required to reach the fitness peak when (1) the net effect of learning on phenotypic fitness is large (in my model this is reflected in learning within a large exploratory range), (2) learning has a fitness cost, and (3) the initial level of learning is higher than the evolutionary optimum. In addition I have found that there exists a critical level of learning above which learning is favoured by selection and evolves towards an optimum level and below which learning is selected against. Moreover above this threshold the joint evolution of learning and innate behaviour is accelerated. In contrast, when the net effect of learning on phenotypic fitness is small (i.e., learning within a small exploratory range), then the evolution of the phenotype proceeds effectively only via changes in the innate behaviour.

Together the theoretical results of my research point to the following conclusions. High levels of adaptive and evolving learning have the potential to accelerate the evolution of an innate trait towards a distant fitness peak (i.e., the evolution of a population that colonizes a novel environment). However when there is a nonzero cost to learning, there exists a threshold below which learning is selected against. Previous theoretical studies of phenotypic plasticity often predict low levels of plasticity in a population adapted to an old and constant environment. Therefore there is no reason to assume a priori high levels of learning when we model evolution in a novel environment. In this setting the evolution of learning critically depends on the cost of learning. In particular, if the cost of learning is too high then the potential for learning to accelerate the evolution of the innate trait is never attained. In contrast, in a constantly varying environment there exist selective pressures maintaining high levels of plasticity.

In conclusion the wealth of theory of the Baldwin effect confirms that adaptive learning may play a positive role in the evolution of innate traits. Relevant questions include: how to estimate the increase in fitness due to adaptive learning, what is the cost of learning in terms of fitness and how adaptive learning influences evolution in a varying environment. Most importantly, these questions await empirical evidence that currently is virtually absent. Such an empirical approach requires a model system where there is genetic variation for both a behavioural trait and the ability to learn. The experimental studies presented in this thesis concerning the response of predatory mite *P. persimilis* to a herbivore-induced plant volatile indicate that both these requirements are satisfied for this system.