The interplay between genetic and learned components of behavioural traits: olfactory responses of predatory mites to signals contained in a herbivore-induced plant volatile
Sznajder, B.A.

Citation for published version (APA):
Sznajder, B. A. (2010). The interplay between genetic and learned components of behavioural traits: olfactory responses of predatory mites to signals contained in a herbivore-induced plant volatile

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

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: http://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
How adaptive learning affects evolution: reviewing theory on the Baldwin effect

B. Sznajder, M.W. Sabelis & M. Egas

Submitted manuscript

Abstract – We review models of the Baldwin effect, i.e., the hypothesis that adaptive learning (i.e., learning to improve fitness) accelerates genetic evolution of the phenotype. Numerous theoretical studies scrutinised the hypothesis that a non-evolving ability of adaptive learning accelerates evolution of genetically determined behaviour. However, their results are conflicting in that some studies predict an accelerating effect of learning on evolution, whereas others show a decelerating effect. We begin by describing the arguments underlying the hypothesis on the Baldwin effect and identify the core argument: adaptive learning influences the rate of evolution because it changes relative fitness of phenotypes. Then we analyse the theoretical studies of the Baldwin effect with respect to their model of adaptive learning and discuss how their contrasting results can be explained from differences in (1) the ways in which the effect of adaptive learning on the phenotype is modelled, (2) the assumptions underlying the function used to quantify fitness and (3) the time scale at which the evolutionary rate is measured. We finish by reviewing the specific assumptions used by the theoretical studies of the Baldwin effect and discuss the evolutionary implications for cases where these assumptions do not hold.

Key words: the Baldwin effect, fitness landscape, evolution of phenotype, adaptive learning.

In theory the evolution of plastic phenotypic traits may lead to two extreme outcomes where the trait becomes either genetically fixed (and largely phenotypically invariable) or it is entirely shaped by environmental influences. In between these extremes lies a spectrum of outcomes where traits contain a genetic component but they are also, to various degrees, modifiable in response to environmental influences. A recurring question in evolutionary biology is how phenotypic plasticity (i.e., the ability to modify phenotype in response to external or internal influences) may influence the outcome and the rate of evolution (Price et al. 2003; West Eberhard 2005; Crispo 2008) by, for example, creating novel selectable forms that are entirely environmentally induced when
Chapter 5

there is not any genetic basis for such a variant (as in populations that colonize a novel environment). This question is particularly relevant in the face of the growing body of evidence that various forms of plasticity (such as the ability to learn) have a genetic basis (Mery and Kawecki 2002; Dukas 2004) and thus may evolve jointly with the genetically determined phenotype.

In this article we focus on the hypothesis that adaptive learning (i.e., learning that improves fitness) facilitates evolution of the genetic basis for phenotypic traits. This hypothesis has its origins in the arguments put forward by Mark Baldwin (1896, 1902), a contemporary of Charles Darwin. These arguments concern a population that finds itself in a new environment, and thus, presumably, does not contain a genetic basis for the complete phenotype that would be optimal in this new environment (i.e., the phenotype that achieves the highest possible fitness). Baldwin argues that adaptive plasticity allows sub-optimal individuals to acquire higher fitness. Hence, learning improves the survival of the population of such individuals and thus it facilitates that the genetic evolution may proceed. Moreover, he observes that under these conditions there is direct selection for the ability to learn adaptively and, simultaneously, indirect selection for any heritable variation carried by the plastic individuals favoured by direct selection. The central argument of Baldwin is that selection for the ability to acquire a fitter phenotype through learning may coincide with the genetic basis for the fitter phenotype (i.e., these indirectly selected genes provide a basis for a fitter phenotype). If this condition is fulfilled, then the selection for improved learning facilitates adaptive evolution of the genetic basis for the trait. Therefore, adaptive learning is predicted to accelerate evolution.

This hypothesis of Mark Baldwin, known in the literature as the Baldwin effect (Simpson 1953) has spurred numerous theoretical studies whose general approach is to measure the rate of evolution of a genetically determined trait, given different levels of a non-evolving ability to learn adaptively. Their results are ambiguous; some studies provide evidence for an accelerating effect of adaptive learning on evolution (Hinton & Nowlan 1987; Fontanari and Meir 1990; Mayley 1997; Ancel 2000 – the norm of reactions models; Lande 2009), yet others show a decelerating effect of learning on genetic evolution (Papaj 1994; Anderson 1995; Ancel 2000 – the quantitative genetic model; Dopazo et al. 2001; Borenstein et al. 2006).

In this article we analyse the theoretical studies of the Baldwin effect with the aim of explaining how learning yields these two contrasting effects. In order to do so, we analyse how – in these studies – learning influences the relationship between different phenotypes and fitness and thereby influences the evolutionary response to selection. In fact, it is one of the underlying assumptions of the
Baldwin effect that learning changes relative fitness differences among phenotypes by conferring a larger fitness increase to those phenotypes (as well as underlying genotypes) that are already relatively closer to the fitness peak (the selection for the ability to acquire fitter phenotype through learning coincides with the genetic basis for the fitter phenotype). Moreover, we discuss the predictions of the theoretical studies in two distinct evolutionary stages that are characterized by different evolutionary end-points derived from the Baldwin effect. The Baldwin effect concerns the evolution of a phenotypic trait towards a single and distant fitness peak; this process is initially realized through the selection of plastic phenotypes but it is finalized when these plastic phenotypes are substituted by a genetically determined and optimal phenotype (presumably because learning has a fitness cost, Baldwin 1896, Simpson 1953). Hence, the theoretical studies of the Baldwin effect generally estimate the amount of time (in generations) needed for the completion of this entire process, but they also allow to separately analyse (1) the number of generations until the first genetically determined and optimal phenotype appears in the plastic population, and (2) the number of generations until this genetically determined optimal phenotype replaces the plastic phenotypes, (which represents the general idea of staging the Baldwin effect, as first proposed by Simpson 1953). These two evolutionary stages may have different time scales and evolutionary dynamics. Therefore, it is reasonable to derive conclusions about the effect of learning on evolution separately for these two evolutionary stages. In the next section, we begin by analysing the results of the theoretical studies of the Baldwin effect, grouped with respect to the concepts of adaptive learning (or adaptive plasticity in general) and the assumed fitness function. We compare the evolutionary rates in the two stages of the Baldwin effect (as defined above) obtained in these studies, whenever these rates are available.

Models of the Baldwin effect: The concept of adaptive learning and the choice of fitness function

The hypothesis on the Baldwin effect states that evolution of an innate (i.e., genetically determined) trait proceeds faster in populations that harbour plastic individuals, than in populations that harbour none of such individuals. Therefore, the general approach in published studies of the Baldwin effect is to measure the rate of evolution of an innate trait given different levels of a non-evolving ability to learn. However, these studies vary with respect to assumed fitness functions; the fitness landscapes they describe range from a single-peak ‘needle-in-haystack’ type to a single-peak landscape with a gradual slope, or a rugged landscape that contains many fitness peaks of varying heights. Moreover, although they all model adaptive learning (i.e., learning leads to a change of phenotype in the direction of increased fitness) the reviewed studies
In their seminal model reviving interest in the Baldwin effect, Hinton and Nowlan (1987) track the changes in the frequency of the alleles associated with fitness pay-off. The increase in the frequency of the allele associated with superior fitness is taken as a yardstick of adaptive evolution. In particular, genotypes are modelled as byte strings that consist of a number of loci. These loci can contain one of two types of alleles and the genotype that is completely homogeneous with respect to one particular type of the allele is taken to be the optimal one (i.e., confers the highest fitness). The assumed fitness landscape, therefore, is of the unimodal 'needle-in-haystack' type. Adaptive learning is introduced by another allele which is not fixed, but can be switched to the type that confers higher fitness based on a learning algorithm, and individuals are allowed to search for the correct setting of these alleles in a number of trials during their lifetime. The individuals that learn the optimal phenotype are preferentially selected for mating (where the probability of being selected for mating increases with decreasing the number of trials the individuals need to learn the optimal phenotype) and thus have more offspring.

The model shows that such learning dramatically speeds up evolution in the population of individuals capable of learning, a result corroborated by Fontanari and Meir (1990) who analyse evolution on the same fitness landscape, using the same learning protocol but assuming asexual reproduction. In fact, the population lacking an allele for learning (i.e., the ‘unspecified’ alleles that get fixed by learning) cannot find this evolutionary end-point. The explanation for these results is that at least some individuals harbour the set of fixed alleles that is not too different from the optimal one and hence they have a higher chance of finding the correct setting of all ‘unspecified’ alleles by learning within the time specified for learning. In other words, thanks to learning these genotypes (that are already closer to the fitness peak) gain a relatively higher fitness than do the plastic genotypes with fewer correct setting of alleles. These findings are also consistent with the argument of Baldwin that learning confers higher fitness gain to those genotypes that are already closer to the fitness peak and thus accelerates evolution of the genetic basis for the optimal phenotype. Nevertheless, the other observation of the model by Hinton and Nowlan is that ‘unspecified’ alleles are not entirely out-selected and remain in the population, indicating different evolutionary dynamics once the population evolves to the vicinity of the fitness peak. However, this result may also be attributed to the fact that learning in this model has no fitness cost.

Chapter 5

of the Baldwin effect use different methods and assumptions to achieve such an effect of plasticity in their model systems.
The study by Mayley (1997) provides evidence that the cost of learning plays a critical role in the interplay between learning and genetic evolution. It also examines in more detail the relationship between the complexity of a fitness landscape and the effect of learning on evolution. In particular, the author compares the movement of a plastic population on unimodal and rugged (i.e., many fitness peaks of varying height) fitness landscapes. In his model, a genetically determined phenotype, represented by a point on the fitness landscape, is considered to evolve if it moves in the direction of the fitness peak. Mayley finds that there is no evolution on a unimodal fitness landscape if learning is cost-free because the optimal phenotype is acquired entirely by learning. Adaptive evolution on a unimodal fitness landscape is only possible, when there is a cost of learning. Yet, on a rugged fitness landscape the population evolves irrespective of the cost of learning. Mayley’s results demonstrate that learning is more likely to facilitate evolution on a rugged fitness landscape, i.e., where there is more than one fitness peak and/or, initially, learning allows the phenotypes to reach only the local fitness peaks but not the global fitness peak (i.e., modifies the phenotype such that it has the highest possible fitness). Moreover, in both the unimodal and rugged fitness landscapes the cost of learning is critical for the convergence of the population on the single optimal genotype, i.e., the genotype whose fitness cannot be improved by learning.

Borenstein et al. (2006) constructed a rugged fitness landscape characterized by a number of local fitness peaks of steadily increasing heights and one global fitness peak. In their model the population continues evolving towards the global optimum by crossing the intermediate fitness valleys and converging on local fitness peaks. The authors measure the rate of evolution as the time it takes the population to reach the global fitness peak and they approximate adaptive learning through the application of an algorithm which allows a learning genotype to repetitively explore the fitness landscape and to modify its phenotype according to the detected fitness gains. This learning process stops when continuation of sampling and learning cannot secure further fitness gains (i.e., the genotype has found the local fitness peak). As a consequence of this learning process all genotypes of the population acquire the same fitness, determined by the local fitness peak, because they all are equally capable of learning. This way of modelling the phenotypic effect of learning is more akin to the way learning is modelled in a series of models due to Hinton & Nowlan, (1987) and Mayley (1997). One feature characteristic to this approach is that genotypes capable of learning can sample potentially large areas of the fitness landscape and modify their phenotypes accordingly. In the model of Borenstein et al. the learning process effectively smoothes the fitness landscape, i.e., it reduces fitness
differences among genotypes. Model simulations carried out by Borenstein et al. confirm that such an effect of learning is associated with slower evolution on a unimodal fitness landscape. However, on a rugged fitness landscape the learning process results in faster evolution because the reduced fitness differences among genotypes help the population to cross fitness valleys, thereby allowing evolution towards the global fitness peak. At the same time, a population of individuals that cannot learn may never be able to cross the fitness valley and find the global optimum. These results prompt Borenstein et al. to conclude that the complexity of the fitness landscape, i.e., the presence of multiple fitness peaks and fitness valleys, determines whether the effect of learning on evolution is accelerating or decelerating.

A separate class of models using the quantitative genetics framework to measure the rate of phenotypic evolution assumes a unimodal fitness landscape (i.e., containing a single fitness peak), given by a Gaussian function (Anderson 1995; Ancel 2000 – quantitative genetics model). These studies introduce an adaptive effect of learning by an increase in the selection variance. Thus the learning process modelled is equivalent to (a small) adaptive shift of the genetically determined trait value of all sub-optimal individuals. This combination of the fitness function and the way of modelling learning results in decreased phenotypic variance and decreased fitness differences among different phenotypes. Moreover, this evolutionary scenario approximates the second stage of the Baldwin effect: the stabilizing selection acting on the population in the vicinity of the fitness peak. Characteristically, these two studies show that learning extends the time required for convergence of the population on the optimal genotype as compared to the evolution in a population with individuals that cannot learn, thus supporting a decelerating effect of learning on evolution.

The same conclusion is drawn by Papaj (1994) in a model that measures the time required for the population to evolve a genetically determined, optimal phenotype (i.e., a genotype that has a highest possible fitness without any learning). This study also assumes a unimodal fitness landscape that is provided by a negative quadratic function (shape of inverted parabola). And, as a consequence of adaptive learning, different phenotypes eventually converge on the single fitness peak. Thus, in this study learning also effectively decreases the phenotypic variance and fitness differences among the phenotypes.

Another class of studies involves modelling adaptive plasticity as a norm of reactions. Ancel (1999, 2000), in her norm of reaction model, explicitly addresses the rates of evolution in the two stages of the Baldwin effect, while varying the degree of plasticity reflected in the width of the norm of reaction. The
mid-point of the norm of reactions represents the genetically determined trait value (i.e., the innate trait) while the phenotype with highest fitness within this range (based on the fitness function) represents the phenotype acquired through learning. Thus, all phenotypes are able to express the optimal phenotype if the norms of reaction of these phenotypes are wide enough to contain the fitness peak (as might be the case when the population is already in the vicinity of this fitness peak), even though there is variation in the innate value in such a population.

On the other hand, setting the initial width of norms of reactions such that they do not contain the optimum, models a scenario where a population evolves towards a distant fitness peak. Ancel (2000) examines how this plasticity affects the rate of evolution in two types of unimodal fitness landscapes: (1) a spiked landscape where a single genotype scores the highest fitness and all the other genotypes score the same flat fitness (also referred to as the 'needle-in-the-haystack' landscape, as in Hinton & Nowlan 1987), and (2) a Gaussian fitness function. The novel aspect of Ancel’s model is that the width of the norm of reaction is allowed to evolve such that the upper and lower bounds of the norm of reactions may shift from one generation the next. For the two settings of the fitness function, Ancel shows that costly adaptive plasticity generally accelerates the first stage of the Baldwin effect, i.e., it shortens the time required for the first optimal genotype to emerge in the population (Ancel 2000). This effect is associated with the initial selection for the wider norms of reactions (Ancel 1999). In contrast, plasticity decelerates the second stage of the Baldwin effect, i.e., it extends the time between the emergence of the optimal genotype and population convergence on this genotype because the wide norm of reaction effectively allow all individuals to learn the optimal phenotype (Ancel 2000).

These results of Ancel provide further evidence that adaptive learning accelerates evolution in the initial stages of the Baldwin effect, i.e., evolution towards a distant fitness peak. However, the decelerating effect of learning prevails in the second and final stage of the Baldwin effect. The results of Ancel obtained for the two stages of the Baldwin effect are corroborated by the study of Lande (2009) where plasticity is also modelled as a reaction norm evolving under the Gaussian fitness landscape. These two studies are a notable exception in the theory of the Baldwin effect by allowing phenotypic plasticity to evolve jointly with the innate trait (see also studies in the framework of artificial life/intelligence, e.g., Watson and Wiles 2002, Suzuki and Arita 2004).

Thus, the theoretical studies indicate that the effect of learning on evolution in not constant as the population evolves on a fitness landscape towards a
distant fitness peak. Therefore it is reasonable to conduct a comparative analysis of the theoretical studies of the Baldwin effect on the studies that measure evolution within the same evolutionary stage (and at the same time scale). In fact, any long-term measure of evolutionary rate (such as, e.g., the time until a first genetically determined optimal phenotype appears in a population) is a net effect of the evolutionary responses occurring at each generation during evolution towards an evolutionary end-point. It is informative, therefore, to analyse how learning may influence this short-term rate of evolution occurring from one generation to the next. This is the approach used in the recent model by Pænke et al. (2007) and in the next section of this article we analyse the approach and results of this model.

Adaptive learning and the response to selection

Pænke et al. (2007) analyse how a population’s response to directional selection changes with improved adaptive learning (or some forms of developmental noise). To this end, the authors analyse how the relationship between phenotype and fitness changes as adaptive learning is improved. In particular, the authors compare the rate of evolution of the innate trait at two different and fixed levels of plasticity and analytically demonstrate that improved adaptive plasticity strengthens the response to selection (and thus accelerates evolution) when it magnifies fitness differences among phenotypes: this is reflected in the steeper relationship between phenotype and fitness. Conversely, improved adaptive plasticity weakens the response to selection (and thus decelerates evolution) when it reduces fitness differences among phenotypes: this is reflected in the lower slope of the function relating phenotype and fitness.

By assuming a non-evolving learning ability, the authors entirely focus on the evolution of the innate trait (although in this model the evolution of adaptive learning may also be incorporated, thus introducing a second axis for the evolution of the phenotype). This allows them to derive a correspondence between their general result as presented above and specific properties of the fitness function (evaluated only in the direction of innate trait) reflected in the shape of the fitness function. In particular, the authors predict that learning magnifies fitness differences among phenotypes when the fitness landscape (evaluated in the direction of the innate trait) is convex. Conversely, adaptive learning reduced fitness differences among phenotypes when this fitness landscape is concave. The authors extend this analysis by assuming various specific functions for the innate phenotype and non-evolving adaptive plasticity, such as used in Ancel (2000) or Andersson (1995) to demonstrate that there exists a fitness landscape on which adaptive learning, as it is modelled, accelerates evolution.
The predictions of Paenke et al. (2007) are derived under the assumptions that the selection is directional (i.e., fitness consistently increases with the value of the innate trait) and non-evolving learning equally modifies different phenotypes (the authors point out that a form of learning that is dependent on the distance of the innate phenotype from the fitness peak may lead to novel predictions). Other assumptions of this framework include the assumption that there are no non-additive or dominance effects shaping the expression of the phenotype, or that there is no genetic covariance between the innate trait and adaptive plasticity.

The approach in the study of Paenke et al. (2007) provides an elegant demonstration of how adaptive learning influences the short-term rate of evolution, i.e., the response to selection measured from one generation to the next when learning is kept fixed. However, allowing the evolution of adaptive learning ability may change the long-term dynamics if the curvature of the fitness landscape is not overall uniform (which is assumed in the model of Paenke et al. 2007).

In summary, the results of Paenke et al. (2007) allow for the conclusion that the effect of adaptive learning on evolution depends on the shape of the fitness function as well as the model of adaptive learning. In particular, adaptive change due to learning that is large relative to the distance of the innate trait from the fitness peak (such that optimal (or nearly optimal) phenotype can always be learned), is more likely to decelerate evolution of the innate trait irrespective of the curvature of the fitness landscape. This theoretical possibility may be unlikely, however, given that in a population adapted to an old environment (that is distant from the new fitness peak as argued in the Baldwin effect), low levels of plasticity are expected (Lande 2009), particularly if plasticity has a fitness cost. There may be selection to maintain high levels of plasticity in a population if there are frequent changes of environment (Stephens 1991). However, in such a theoretical situation the environment (and thus a fitness landscape) is dynamical, while the theoretical studies of the Baldwin effect generally assume a constant environment (and thus a constant fitness landscape).

Conclusions
The effect of adaptive learning on evolution of genetically determined traits is the subject of a long-standing debate and the theoretical treatments of this question provide contrasting results. Here, we discussed how these contrasting results can be partly explained from the different ways in which the theoretical studies measure the evolutionary rate. The traditional end-point of the Baldwin effect is the complete convergence of a population on an initially distant fitness peak associated with reduction in the level of adaptive learning. Adaptive learn-
Chapter 5

Learning is considered to accelerate evolution if it helps to reach this end-point faster. This measure however may fail to adequately describe the effect of learning on evolution if this effect is not constant but changes as the population evolves on a fitness landscape (particularly, a rugged fitness landscape). A measure of short-term evolutionary change as occurring from one generation to the next may be better suited to detect the variable effect of learning on evolution. The recent study by Paenke et al. (2007) provides such a framework where such a measure is employed to demonstrate how learning influences fitness differences among different innate phenotypes, thus either accelerating or decelerating the evolution of the innate phenotype. By relating the effect of learning on fitness differences among phenotypes to the shape of the fitness function (that determines these fitness differences) the authors demonstrate how theoretical predictions of the Baldwin effect depend on the choice of fitness functions. However, our analysis of this and other theoretical studies of the Baldwin effect indicates that the model of adaptive learning (i.e., how learning is modelled to change the innate phenotype) also matters to the theoretical predictions.

By definition adaptive learning modifies the phenotype so as to increase its fitness. However, adaptive learning may be characterised with respect to how much it modifies the innate phenotype given the distance of this innate phenotype from a fitness peak. In other words, the magnitude of the phenotypic modification due to learning can be modelled as either a small or a large step in phenotype space, depending on the size of the exploratory range attributed to the individuals. In particular, simulation models (Hinton & Nowlan 1987; Mayley 1987; Borenstein et al. 2006) employ learning which allows the genotype to sample large areas of a fitness landscape in search of a local fitness peak. In this process, phenotypes are allowed to experience many learning trials during their lifetime (as in Hinton & Nowlan 1987; Fontanari and Meir 1990) or adaptive search is repeated until phenotypic fitness can no longer be improved (Mayley 1997; Borenstein et al. 2007). Therefore, the optimal phenotype can be learned by all phenotypes. In contrast, in another class of models (Anderson 1995; Ancel 2000 – quantitative genetic model) adaptive learning effectively involves a relatively small (with respect to the distance of the innate trait from the fitness peak) adaptive shift of the innate trait in the direction of increased fitness. This phenotypic modification is assumed to be fixed (i.e., the magnitude of the shift cannot be increased/decreased in response to the fitness gains determined by the fitness function) and the resulting learned phenotype may not be very different from the genetically determined one. This distinction between the two ways of approximating adaptive learning, based on the potential of learning to modify the phenotype, is relevant because each of the two modes of learning has distinct consequences for the fitness of individual pheno-
types. This may be particularly relevant in the case of evolution on a rugged fitness landscape. Adaptive learning that has a large potential to modify the phenotype is exemplified by unconstrained adaptive search of the fittest options on the fitness landscape. We argue that the effect of such learning on evolution is less likely to depend on the local curvature of the fitness slope because it allows genotypes to sample distant areas of the fitness landscape. On the other hand, adaptive learning modelled as a small shift of the phenotype is much less likely to allow the population to cross fitness valleys and find a global fitness peak.

Current theory is based on the assumption that learning is a fixed trait, and concentrates on tracking evolution of the genetically determined component of a phenotype. This assumption is challenged by the empirical evidence showing that adaptive learning can be successfully subjected to artificial selection (e.g., Mery and Kawecki 2002). It remains to be shown how the current theoretical predictions change if adaptive learning is allowed to evolve jointly with the genetically determined trait value. Moreover, although not considered in the theory on the Baldwin effect, the mechanism of learning may not always be adaptive (as in the case of non-associative mechanisms of learning) and may give rise to entirely different evolutionary dynamics.

The Baldwin effect concerns the evolution towards a distant fitness peak; hence the assumption of the fitness landscape, where the innate trait is under directional selection and evolves towards a distant optimum whose position in the landscape is constant in time. It remains to be explored how adaptive learning influences evolution of the genetic basis for phenotypic traits on a dynamic fitness landscape because, for example, the environment changes frequently or the optimal phenotype depends on the frequency of other phenotypes in the population.

Theory has shown that the cost of learning plays a crucial role in the evolutionary dynamics of traits modified by learning. Experimental evidence for costs of learning are only beginning to emerge (Mery and Kawecki 2003; or the cost of phenotypic plasticity see Auld et al. 2010), yet they are essential to motivate biologically realistic cost functions in the theoretical models of joint evolution of learning and innate behaviour. Any cost of learning determines the evolution of learning and, therefore, it will play a particularly relevant role in any model of joint evolution of adaptive learning and innate behaviour. Another common assumption awaiting empirical scrutiny is that all genotypes are equally capable of learning. This, however, need not be the case and theoretical predictions may change entirely if the level of learning is variable for different genotypes (for example, if there is a correlation between the genetically determined trait value and the level of learning as discussed in Mery and Kawecki 2004).
Chapter 5

To date, empirical evidence for a role of learning in evolution is virtually absent (but see Mery and Kawecki 2004). An empirical approach requires a model system where genetic variation for both a behavioural trait and the ability to learn are demonstrated, and where the level of learning and the innate value of the behavioural trait can both be quantified as separate traits.

References
How adaptive learning affects evolution


