

The effect of learning on the evolution of new courtship behavior: A simulation model

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Abstract The fact that individuals learn can change the relationship between genotype and phenotype in the population, and thus affect the evolutionary response to selection. Here we ask how male ability to learn from female response affects the evolution of a novel male behavioral courtship trait under pre-existing female preference (sensory drive). We assume a courtship trait which has both a genetic and a learned component, and a two-level female response to males. With individual-based simulations we show that, under this scenario, learning generally increases the strength of selection on the genetic component of the courtship trait, at least when the population genetic mean is still low. As a consequence, learning not only accelerates the evolution of the courtship trait, but also enables it when the trait is costly, which in the absence of learning results in an adaptive valley. Furthermore, learning can enable the evolution of the novel trait in the face of gene flow mediated by immigration of males that show superior attractiveness to females based on another, non-heritable trait. However, rather than increasing monotonically with the speed of learning, the effect of learning on evolution is maximized at intermediate learning rates. This model shows that, at least under some scenarios, the ability to learn can drive the evolution of mating behaviors through a process equivalent to Waddington's genetic assimilation [*Current Zoology* 61 (6): 1062–1072, 2015].

Keywords Baldwin effect, Genetic assimilation, Learning and evolution, Sensory drive, Sexual selection

Numerous mathematical models and computer simulations (e.g. Hinton and Nowlan, 1987; Fontanari and Meir, 1990; Papaj, 1994; Ancel, 2000; Borenstein et al., 2006; Paenke et al., 2007; Sutter and Kawecki, 2009; Kawecki, 2010) indicate that the ability of individuals to learn can affect evolutionary change in the population, a notion first verbally proposed 120 years ago (Baldwin, 1896; Osborn, 1896). That learning can both slow down and accelerate genetically-based evolutionary change has also been demonstrated with experimental evolution (Meryand Kawecki, 2004). The general reason why learning can affect evolution is simple: adaptive evolution is driven by the relationship between genotype and phenotype (heredity) and between phenotype and fitness (selection); learning can affect both these relationships. It can also affect population structure (e.g. via habitat or mate choice) and thus the amount of gene flow between sub-populations exposed to differential selection. In other words, "learning alters the shape of the search space in which evolution operates" (Hinton and Nowlan, 1987). Thus, despite claims on the contrary (e.g. Laland et al., 2014), the effect of learning on evolution can be well understood and analyzed within the framework of existing evolutionary theory (Ghalambor et al., 2007;

Paenke et al., 2007).

In most biologically realistic scenarios, learning will allow individuals farther from the optimum to compensate for the deficiencies of their genetic makeup, thus reducing variation in fitness (flattening the fitness landscape). This buffering effect is expected to slow evolutionary change (Ancel, 2000; Paenke et al., 2007). However, under some conditions individuals genetically closer to the optimum may benefit proportionally more in term of fitness from learning than those farther away. This effectively amplifies the strength of selection at the level of the genotype, and thus is expected to make the selection more effective (Hinton and Nowlan, 1987; Fontanari and Meir, 1990; Paenke et al., 2007; Kawecki, 2010). This is in turn expected to accelerate the response to selection, or even change the direction of evolution e.g. if the fitness landscape contains an "adaptive valley" (Borenstein et al., 2006). It is thus of interest to explore under what specific biological scenarios learning is expected to amplify the strength of selection.

The potential influence of learning on evolution has received particular attention in the context of sexual selection. Much of that work (reviewed by Verzijden et al., 2012; see also Servedio and Dukas, 2013) focused

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on social and individual learning affecting mate preference (e.g., mate-copying or learning about phenotypes of available mates). A general prediction from those studies is that learning of mate preferences should facilitate divergence in mate preference between populations under a broad range of biologically realistic conditions. The predictions have been more mixed for social learning of courtship traits (such as bird song) by imitating other individuals (Ellers and Slabbekoorn, 2003; Lachlan and Servedio, 2004; Olofsson et al., 2011; see Verzijden et al., 2012 for their summary). In contrast, individual instrumental learning of courtship traits, where an individual modifies its behavior in response to a feedback (reinforcement) (Bouton, 2007), has received little attention in the context of the effect of learning on evolution driven by sexual selection. In response to this gap, one of us (Kawecki, 2013) proposed a verbal scenario under which individual learning of a courtship trait might expedite the evolution of a novel courtship trait under pre-existing female sensory bias. The present study uses individual-based simulation model to verify the verbal model proposed by Kawecki (2013), study the conditions under which it holds, and extend it to the case of gene flow from a population expressing a different courtship trait.

A key assumption of our model is that female response to male courtship is not all-or-none (i.e., mating or ignoring). Rather, we assume that males above a certain threshold of attractiveness (as determined by their courtship behavior) elicit responses from females (e.g., they may be approached and inspected). Many of those males that get a look-in but do not meet another, higher attractiveness threshold will be rejected as mates. However, these males of intermediate attractiveness will be able to learn from that initial female response that a particular behavior attracts females, and will enhance this behavior in the future. Thus, another key assumption we make is that males are able to use female response as positive reinforcement (a reward) in instrumental learning (Bouton, 2007). Thus, upon the next encounter with a female, the male expression of the courtship behavior – and thus his attractiveness – will increase, possibly eventually passing the threshold for mating. While it is biologically realistic to expect that females will exhibit a continuum of responses to male courtship and other phenotypes, this two-step model of male-female interactions captures the essence of that variation while remaining simple. A prediction, formulated verbally by Kawecki (2013) is that, under a broad range of conditions, males that already have a relatively

high innate expression of the courtship trait will benefit more from learning the courtship trait simply because they need fewer rounds of learning to achieve courtship performance that exceeds the females' requirement for mating.

We consider a scenario in which females show a pre-existing attraction to a particular courtship behavior (i.e., sensory drive; Endler, 1992; Boughman, 2002), and the courtship behavior is the only trait that evolves (i.e., is genetically variable). We are mostly interested in cases where this trait is novel, i.e. where the genetic component of the courtship trait is low, so that most naïve males express it at a rudimentary level, well below the threshold that elicits female acceptance for mating. We assume that no other courtship trait or sexual ornament is expressed by males in the focal population. As proposed by Kawecki (2013), this may follow an environmental change or colonization of a new environment, in which pre-existing courtship traits are ineffective or not expressed (e.g., a carotene-based trait in an environment devoid of dietary carotene). Consistent with this sensory drive scenario, in a subset of simulations we consider gene flow from another (source) populations, whereby the immigrant males, having developed in another environment, still express an old courtship trait that the local females find attractive. Alternatively, the immigrant males may be attractive simply because they are unfamiliar to females ("rare male effect"; Graber et al., 2015). However, because the sons of the immigrant males develop in the local environment, they do not enjoy the mating advantage any more.

1 The model

We implemented an individual-based model in Python version 2.7 (www.python.org). We consider a sexual diploid species with non-overlapping generations. The population size is regulated at $N = 2500$ adult individuals with a 50:50 operational sex ratio. The life cycle consist of three stages: (i) a mating season, with multiple encounters between males and females, and (ii) generation of progeny, involving recombination of parental haplotypes and mutation, and (iii) recruitment of juveniles to the adult population, involving viability selection. No spatial structure is assumed within the population, i.e., any female of this population can encounter any male at random. However, in one model variant we consider immigration of adults from another population occurring before mating (see below).

1.1 Sexual selection and courtship learning

Each female is assumed to mate only once, but males

may mate multiply. Males express a behavioral courtship trait X ($0 \leq X$); it can be thought of as the intensity of a particular type of courtship. During the reproductive season, females encounter males at random. The female's response depends on the male's courtship trait X relative to two threshold values, the inspection threshold T_I , and the mating threshold T_M . In all simulations presented in the Results we assume $T_I = 0.2$ and $T_M = 0.8$. If $X \leq T_I$, the female will ignore the male, if $X > T_I$, the female will be attracted to the male and thus will inspect/respond to his courtship. If the male courtship trait exceeds another, higher threshold ($X > T_M$, where $T_M > T_I$), the female will mate with the male. However, even if the female does not find the male to her satisfaction (i.e., if $X \leq T_M$), the female will mate with this male with probability H , irrespective of the male's phenotype. If a female has mated, she is removed from the mating pool (and thus ceases to respond to males). If a female does not mate upon meeting a male, she remains in the mating pool but her probability to mate at random with the next male irrespective of his courtship trait increases according to

$$H_{t+1} = H_t + a, \quad (1)$$

Where $H_0 = 0$ and a is the parameter that quantifies the female's persistence in being choosy (greater a means less persistent females; all parameters of the model are listed in Table 1).

Thus, with each successive encounter, females which did not mate yet become less choosy. This assumption is justified on adaptive grounds – remaining highly choosy in the absence of preferred mates would mean that the female does not find a mate and thus leaves no offspring – and is supported by evidence (e.g., Fowler-Finn and Rodriguez, 2012). The number of encounters with males is unlimited, i.e., females continue to encounter males until all females have mated.

The initial (innate) value of the courtship trait, X_0 , is

determined by eight autosomal, independently segregating loci with two alleles ("1" and "0") and with equal and additive effects, whereby each "1" allele increases the trait value by 1/16 (these loci are not expressed in females). Additionally, a non-heritable component ε representing developmental noise (i.e., non-heritable random variation), sampled from normal distribution with zero mean and standard deviation σ ; values that would be negative are set to zero:

$$X_0 = \max[(\text{number of "1" alleles})/16 + \varepsilon, 0]; \quad (2)$$

The number of "1" alleles/16 is thus the genotypic value of the courtship trait and ε is an environmental deviation. In most simulations we assume that the developmental noise is low ($\sigma = 0.025$), but we also explore the consequences of increasing it. The courtship trait can be modified by learning, i.e. it becomes reinforced when the male is inspected by a female. That is, when $X > T_I$, the courtship trait value the male will express in his next encounter with a female will be

$$X_{t+1} = X_t + L, \quad (3)$$

where L is the rate (speed) of learning. In contrast, when $X \leq T_I$, the value of X remains unchanged (even if the female mated with that male, which happens with probability H as described above). Equation (3) implies that female inspection response continues to act as a positive reinforcement for the male over consecutive encounters even if it the response does not culminate in mating. All males remain in the mating pool irrespective of how many times they have already mated.

1.2 Off spring generation and viability selection

Gametes are generated by random and independent recombination of both haplotypes of a parent. Mutations occur in gametes with a probability (genomic mutation rate) of $\mu = 0.001$ per gamete; they are implemented by assuming that in fraction μ of gametes the allele will change to the alternative one (i.e., '0' to '1' or '1' to '0') at a random locus. To generate offspring, a female is chosen

Table 1 Parameters of the model; "default" values used in most simulations are in bold

Symbol	Meaning	Values explored
N	Breeding population size	2500
L	Learning rate	0, 0.04, 0.08, 0.16, 0.32
a	The rate with which female tendency to mate at random increases with successive encounters	0.05 , 0.15, 0.5
σ	Standard deviation of the developmental noise	0.025 , 0.1, 0.25
μ	mutation rate	0.001
s	Survival cost of the courtship trait	0 , 1.5, 3
m	Immigration rate	0 , 0.01, 0.05
T_I	Threshold value of the courtship trait that elicits female inspection	0.2
T_M	Threshold value of the courtship trait that elicits mating	0.8

at random (with replacement) from the pool of mated females, and an offspring is generated by combining a random gamete of the female with a random gamete of the male with which she mated. This is equivalent to assuming that all females contribute equally to the offspring pool, irrespectively of their genotype and the genotype or phenotype of their mating partner. Sex of the offspring is assigned at random. All female offspring are recruited to the adult pool (this is equivalent to assuming a probability of recruitment that is independent of the genotype); for male offspring, we implement a viability cost of the courtship trait: the probability of being recruited is $\exp(-sX_0)$. Thus, parameter s quantifies the strength of viability cost of the innate value of the courtship trait. The process is repeated until $N/2$ individuals of each sex are recruited. All adults die after reproduction.

1.3 Genetic evolution of the courtship trait

At the beginning of each simulation run, the N initial individuals are sampled from a population with a given allele frequency (the same at all loci, in most cases 0.2), at linkage equilibrium and Hardy-Weinberg proportions. Our main interest is to study the effect of male learning as quantified by the learning parameter L , on the genetic evolution of the innately expressed courtship trait X_0 . We describe the results in terms of the mean genotypic value of trait X in the population; because of the equal and additive genetic effects this mean genotypic value equals the average frequency of "1" alleles across loci. The effect of parameters on the evolution of the courtship trait is in part expressed in terms the number of generations it takes for the genotypic value of trait X to increase from the initial value to above the females' mating threshold (T_M). We refer to this as the "time to establishment" of the trait in the population. The simulations were run for the maximum 10,000 generations; for the parameter sets reported this was sufficient for the trait either to become established as defined above (mean genotypic value $>T_M$), or to converge close to an apparent equilibrium/attractor below T_M . We performed multiple runs for each parameter set and report the average behavior. Figure 1 shows an example of this dynamics, also illustrating the variation among replicate runs (this degree of variation is typical for all results reported here). In the Results section we report the trajectory of the genotypic value of trait X averaged over multiple runs (between 10 and 30), and, where appropriate, the mean and standard deviation of the time to establishment of the trait.

1.4 Gene flow

Most results we report below are obtained for an isolated population. However, in a metapopulation setting, the evolution of a new courtship trait can be hampered by gene flow; evolution of courtship trait distinct from the ancestral population is a potential pathway to speciation (Butlin et al., 2012; Verzijden et al., 2012). We therefore also explore how learning can affect the evolution and maintenance of the new courtship trait in the face of gene flow from another population, in which the trait is not selected for. Immigration, quantified by immigration rate m , occurs at the adult stage before mating; i.e., in each generation mN individuals of both sexes in the mating pool are immigrants. The immigrants are sampled from a population with frequency of alleles "1" equal to 0.2 at all loci, at Hardy-Weinberg proportions and linkage equilibrium. Furthermore, immigrant males are highly attractive to the females, so the local females automatically accept to mate with any immigrant male; however, this attractiveness is not heritable. This assumption corresponds to the original scenario envisioned by Kaweckı (2013), where the focal population was supposed to have colonized a novel environment where an older courtship trait could not be expressed (such as carotene-based coloration in an environment that lack carotene). The immigrant males, having developed in the ancestral environment, would still express the old trait and thus be attractive to the local females.

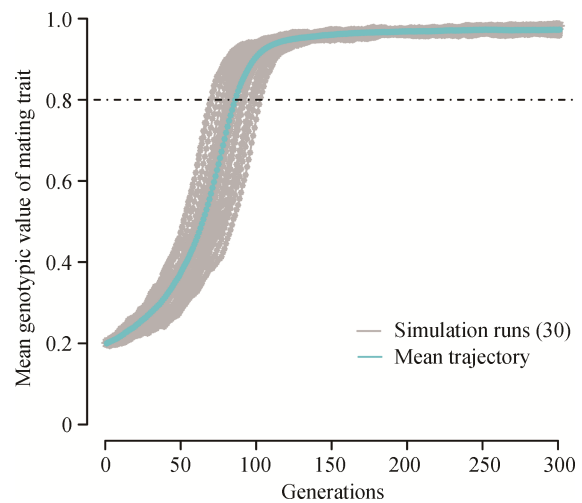


Fig. 1 An example of the evolution of the courtship trait, expressed in terms of its mean genotypic value (i.e., the mean frequency of alleles "1" across loci)

Thirty replicate simulation runs (in grey) and their average (in cyan) are shown for $L = 0.16$ and $\alpha = 0.5$. "Establishment" of the courtship trait is defined by genotypic value exceeding 0.8 (horizontal dashed line).

2 Results

2.1 Effect of learning and female persistence in choosiness

Figure 2 illustrates the effect of the learning rate (parameter L) on the rate of genetic evolution of the courtship trait from an initially low frequency of alleles "1" (0.2). In the absence of learning ($L = 0$) and with low developmental noise ($\sigma = 0.025$) the rate of evolution of the courtship trait is very slow. This is because with low mean X_0 , very few males exceed the threshold for mating; thus, most females, having failed to find a preferred male, eventually mate at random (Fig. 3A). In contrast, when the males are capable of learning from the female

response, those with $X_0 > T_l$ will upregulate the expression of their courtship trait after each encounter with a female, eventually exceeding the mating threshold T_M (Fig. 3B). Thus, the fitness of males with high innate courtship trait is improved by learning, whereas the fitness of males with $X_0 \leq T_l$ is not – because females pay no attention to them, they do not have the opportunity to learn what behavior females find attractive. The resulting fitness difference markedly accelerates the evolution of the courtship trait. However, the relationship between the rate of evolution and the learning rate is U-shaped rather than monotonic (Fig. 2B). This is because, with moderate learning, only males whose innate expression of the courtship trait is already close

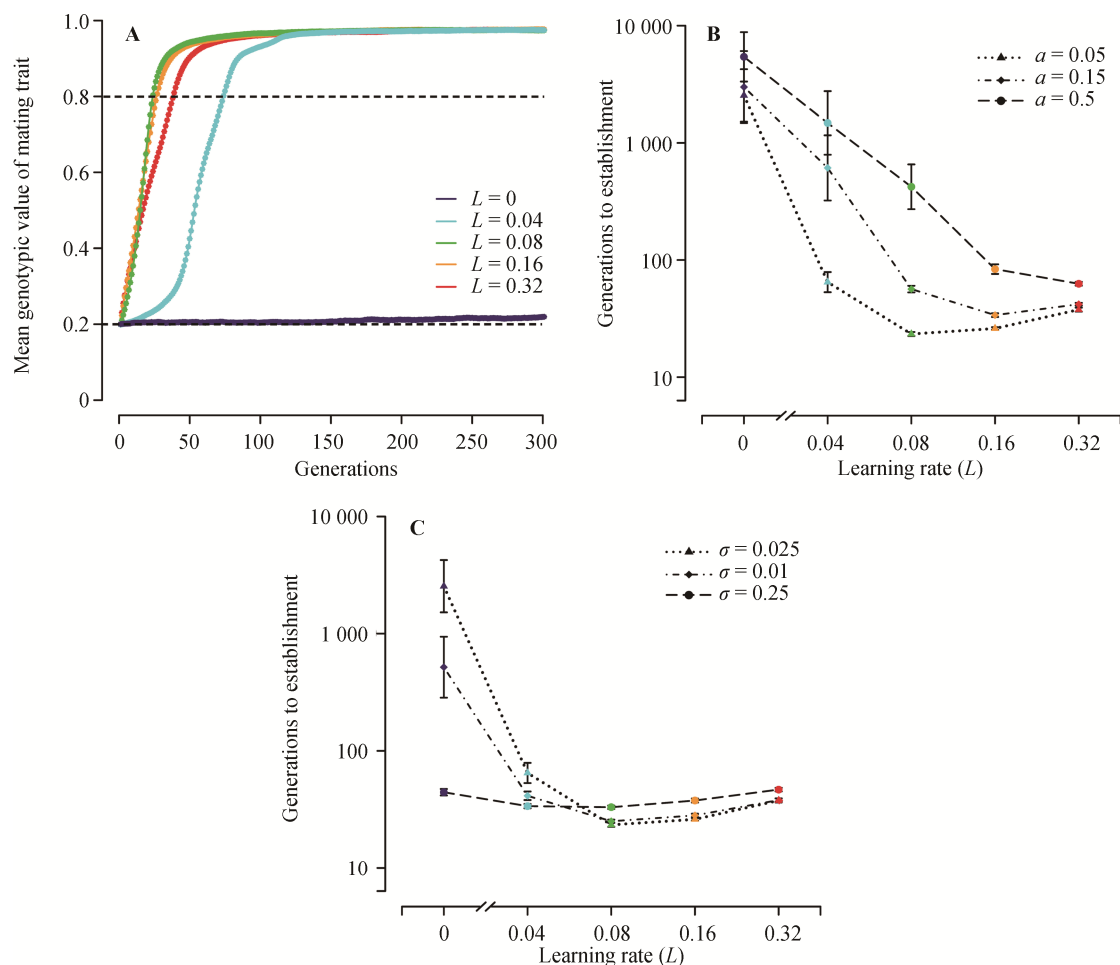


Fig. 2 The effect of learning on the genetic evolution of the courtship trait in the absence of costs and immigration

A. The average trajectory of the genotypic value of the trait (i.e., the mean frequency of the "1" allele across loci) under different values of the learning rate L (assuming $a = 0.05$). **B.** Time to the establishment of the trait in the population (defined as the time needed for the mean genotypic value to increase from the initial 0.2 to 0.8) as depending on the learning rate L and the parameter a , which describes the females' persistence in searching for the preferred male (low a = high persistence). **C.** The interaction between the effects of the learning rate L and the random developmental noise σ on the establishment of the courtship trait. $a = 0.05$ is assumed, i.e., the dotted line represents the same results as the dotted line in panel B. In panels B and C the symbols are means of replicate runs \pm standard deviation (30 replicates per set for times of establishment < 300 ; 10 replicates per set for times of establishment > 300). Where the error bars are not visible, they are smaller than the size of the symbol. Confidence intervals for the mean time to establishment are always narrower than the standard deviation error bars shown. For each value of parameter a (in panel B) or σ (in panel C), the mean time to establishment differs significantly between any pair of L values at $P < 0.05$ (Wilcoxon test).

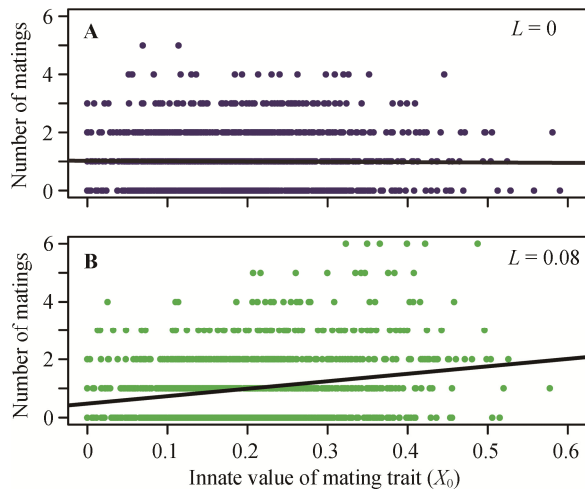


Fig. 3 An example of the effect of learning on the relationship between genotype and fitness

The scatterplots show the relationship between the innate value of the courtship trait X_0 and the mating success in the absence of learning (A) and with a moderate learning rate (B), each from the first generation of a single simulation run. The lines are linear regression (i.e., the fitness gradient). Parameters correspond to Figure 2A (blue and green lines).

to the mating threshold can reach it before females start mating at random; with very fast learning, any males with $X_0 > T_l$ can quickly achieve the mating threshold by learning. This slows down the rate of evolution somewhat, in particular when the mean X_0 is already close to the mating threshold (compare the dynamics between $L = 0.08$ and $L = 0.32$ in Fig. 2A).

Figure 2B also shows that a population with females which have a low tendency to mate at random (i.e., are "patient" looking for a preferred male, meaning a low value of a) is always faster to reach the establishment of the novel trait, for a given learning rate, than a population with females which are less persistent in their preference (large a). This reflects the higher likelihood that the males that took time to learn to express the courtship trait above the mating threshold actually still meet choosy females. In the remainder of results, we assume that females' tendency to mate randomly only increases slowly ($a = 0.05$).

The results in Figure 2A, B were obtained assuming a low degree of developmental noise ($\sigma = 0.025$). This meant that the likelihood of the innate value of the courtship trait X_0 deviating from the genotypic value of the individual by more than 0.1 units was virtually nil (6×10^{-5}). However, sufficiently large developmental noise would extend the tails of the phenotypic distribution, causing some individuals with genotypic value well below the mating threshold to express an innate phenotype above the threshold. Thus, greater developmental noise renders the relationship between the genotypic

value and the likelihood of expressing innate phenotype above the mating threshold more gradual (Figure 4). As Figure 2C illustrates, in the absence of learning ($L = 0$) this markedly accelerates the evolution the courtship trait from a low initial mean value. However, the effects of learning and developmental noise on the evolution of the courtship trait are far from additive – at high learning rates increasing developmental noise actually slows down the evolution of the courtship trait (Fig. 2C).

2.2 Cost of the courtship trait

If the courtship trait is costly in terms of survival to maturity, learning not only affects the rate of its evolution, but also its ultimate outcome (Fig. 5). In particular, with a high cost ($s = 3$), in the absence of learning there is net selection against the courtship trait, leading to elimination of "1" alleles (Fig. 5A). X_0 increases from an initially low value only if the learning rate L is above a threshold. However, if the males learn very fast, the innate expression of the courtship trait evolves towards an intermediate value above the inspection threshold, but below the mating threshold (e.g., Fig. 5A, red line). (Even though the red line in Figure 5A indicates that the mean genotypic value continues to decline by generation 300, we verified that it tends to an equilibrium value of about 0.25). Males with such intermediate values of X_0 avoid paying an excessive survival cost as juveniles – with $s = 3$ males with $X_0 = 0.8$ are 6 times less likely to be recruited than those with $X_0 = 0.2$, but once they become adults their fast learning allows them to increase the phenotype of the courtship trait fast enough to achieve high mating success. So in this situation, high learning allows the phenotype of the courtship trait in the adult population to be high, but inhibits its genetic assimilation. In consequence, only intermediate learning

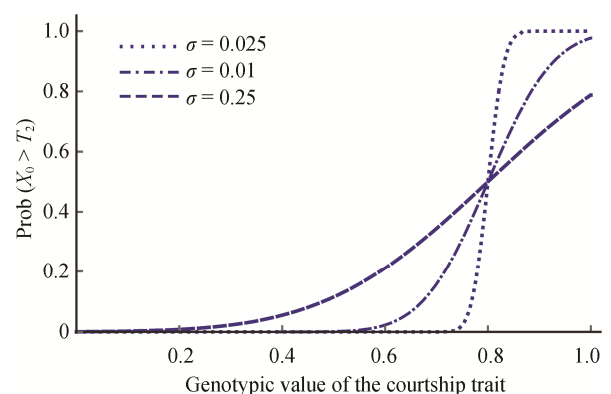


Fig. 4 The effect of developmental noise (quantified by parameter σ) on the relationship between the genotypic value of an individual (the number of "1" alleles divided by 16) and the probability that its innate phenotype of the courtship trait X_0 will exceed the mating threshold $T_M = 0.8$

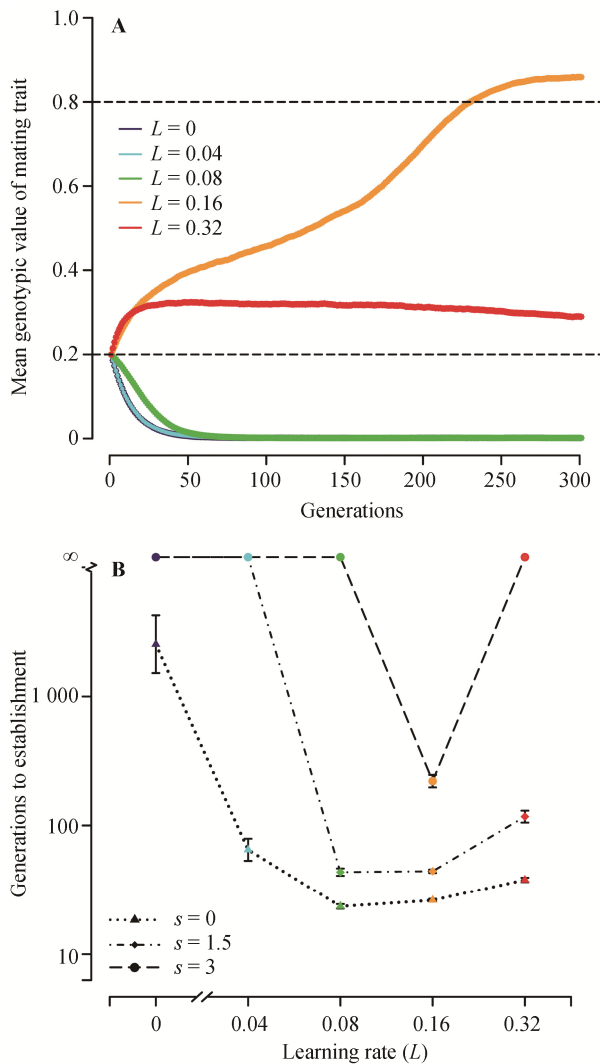


Fig. 5 The effect of learning on the evolution of a costly courtship trait

A. Trajectory of the mean genotypic value for a very costly trait ($s = 3.0$). **B.** Time to establishment of the novel trait as a function of the learning rate L and the cost of the courtship traits. The symbols are means of replicate runs \pm standard deviation (30 replicates per set for times of establishment < 300 ; 10 replicates per set for times of establishment > 300). The blue line (no cost) presents the same results as the blue line in figure 2B; $a = 0.05$ is assumed for all runs in this figure.

rates favor the evolution of the courtship trait to the point where it would exceed the mating threshold (Fig. 5 B). Obviously, further increase of the cost of the courtship trait would lead to elimination of alleles '1' in the focal population irrespective of the learning rate (not shown).

The results in figure 5 were obtained assuming low developmental noise ($\sigma = 0.025$). We reported above that in the absence of learning and with a cost-free courtship trait, increased developmental noise can substantially accelerate the evolution of the courtship trait (Fig. 2 C). However, in simulations with costly trait ($s = 1.5$) and no learning ($L = 0$) the mean genotypic value of the

population evolved towards zero irrespective of whether the developmental noise was low ($\sigma = 0.025$) or high ($\sigma = 0.25$; results not shown). Thus, in contrast to learning, developmental noise does not appear to promote the evolution of a costly courtship trait under the scenario assumed in this paper.

2.3 Immigration from the ancestral population

The results described above considered an isolated population, without migration. Here, we explore the consequences of immigration from an ancestral population in which the mean genetic value of the courtship trait is low. We assume that the frequency of "1" alleles in the immigrant pool is 0.2, but the immigrant males are nonetheless always accepted by the females as mating partners. Figure 6 illustrates the evolution of the innate expression of the courtship trait under immigration rate $m = 0.05$, depending on the learning rate and the initial frequency of "1" alleles (no cost of the courtship trait is assumed). As can be seen from the figure, for the range of parameter values considered, the mean genotypic value of the innate courtship trait does not evolve above the mating threshold of $T_M = 0.8$ (although this does happen with a lower immigration rate e.g., $m = 0.01$; not shown). However, the outcome still strongly depends on the learning rate, in interaction with the initial genotypic value. For moderate to high learning rates ($L = 0.08$ and higher), the genotypic value of the courtship trait converges to an equilibrium value intermediate between 0.2 (inspection threshold) and 0.8 (mating threshold), irrespective of the initial allele frequency (Fig. 6, green, yellow and red lines). In contrast, there are alternative attractors for $L = 0$ and $L = 0.04$. If the initial genotypic value (i.e., frequency of allele "1") is low, sexual selection in the absence of learning is completely ineffective in increasing this frequency above that in the immigrant pool (Fig. 6, blue line starting at 0.2 and 0.5) or with $L = 0.04$ (cyan line starting at 0.2). However, if the initial frequency is high, the allele frequency converges to an equilibrium value somewhat less than 0.8 (blue line starting at 0.8, cyan lines starting at 0.8 and 0.5).

Interestingly, this equilibrium allele frequency declines with increasing learning rate. Given the stochastic nature of the simulations, it is plausible that simulation runs starting from the same initial allele frequency could converge to one or the other equilibrium if the initial allele frequency were close to the border between their basins of attraction. This was, however, not observed for the parameter values and initial frequencies reported – replicate runs starting from the same initial allele frequency showed very similar dynamics, not more varia-

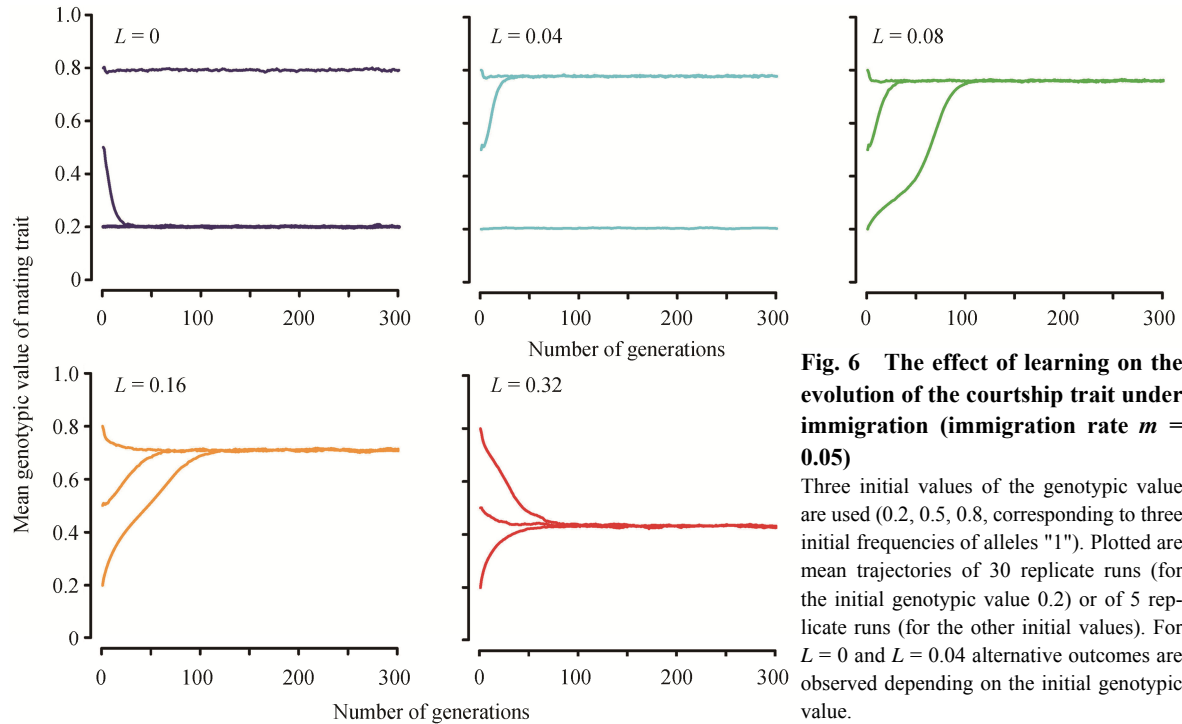


Fig. 6 The effect of learning on the evolution of the courtship trait under immigration (immigration rate $m = 0.05$)

Three initial values of the genotypic value are used (0.2, 0.5, 0.8, corresponding to three initial frequencies of alleles "1"). Plotted are mean trajectories of 30 replicate runs (for the initial genotypic value 0.2) or of 5 replicate runs (for the other initial values). For $L = 0$ and $L = 0.04$ alternative outcomes are observed depending on the initial genotypic value.

ble than illustrated in Figure 1.

We interpret these equilibria as a balance between the genetic load resulting from gene flow and the learning ability of the individuals. Immigration from ancestor population generates many "hybrids" because immigrant males have a high mating success. However, the "hybrids" will usually have rather low innate courtship trait value (because one of their parents came from the source population with low genotypic value). We suggest that those differences in reproductive success of the locals, hybrids and immigrants lead to the pattern of equilibrium observed for sufficiently high learning rate. A high learning rate will allow a greater proportion of hybrids to compensate for their weak innate trait expression and still reach mating threshold. So, with high learning, the genetic load due to immigration is only inefficiently removed by sexual selection from the focal population's genetic pool. Thus, learning facilitates the genetic evolution of the courtship trait from a low value in the face of gene flow, but once the population has diverged, it is predicted to remain more diverged if there is no learning.

3 Discussion

With this simulation model we aimed to illustrate how male ability to learn from individual experience about mating behaviors that females find attractive can affect the genetic evolution of a novel mating behavior. We find that, under the scenario assumed in the model,

learning can promote the evolution of a novel courtship trait. For a broad range of parameters, the new trait evolves faster with than without learning. More importantly, under some assumptions (cost of the courtship trait, gene flow), the novel trait only evolves from a low initial value if the males are capable of learning. Thus, the learned expression of the novel courtship trait acts in our model as a stepping-stone in its evolution towards the point where it is expressed even by naïve males.

Such an expediting/facilitating impact of learning on evolutionary change has been termed "Baldwin effect" (Simpson, 1953; Waddington, 1953; Hinton and Nowlan, 1987), named after the first proponent of this idea (Baldwin, 1896). The process by which it happens is analogous to genetic assimilation of morphological traits in Waddington's classic experiments (Waddington, 1952). As shown by Paenke et al (2007), the Baldwin effect requires that individuals whose genotypic values are already closer to the optimum benefit proportionally more from learning in terms of fitness. In our model this occurs through two main mechanisms. First, only males whose innate expression of the courtship trait is above the threshold value that attracts the attention of females get the chance to learn. Second, of males that pass this inspection threshold, those with a higher innate expression of the courtship trait will pass the mating threshold after fewer encounters with females – and thus will enjoy a quantum jump in fitness. A similar threshold rela-

tionship between phenotype and fitness (or a strongly accelerating one) has been found to promote the Baldwin effect in other models (Hinton and Nowlan, 1987; Fontanari and Meir, 1990; Paenke et al., 2007).

However, our model also predicts situations in which learning reduces the strength of sexual selection at the genotypic level. This occurs when learning allows most males to reach the mating threshold after a single or a few interactions with females. This requires that the learning rate is high and the mean genotypic value of the courtship trait is already close to the mating threshold. As a consequence, while learning generally accelerates the initial evolution of the courtship trait, under high learning rates evolutionary change is slowed down as the mean genotypic value approaches the mating threshold. Intermediate learning rates are thus predicted to be the most favorable for the evolution of the novel courtship trait – they allow sexual selection to act on the range of intermediate genotypes with a higher resolution.

Much of previous work on the potential effect of learning on the outcome of sexual selection has been done in the context of speciation (Verzijden et al., 2012). Therefore we also considered a scenario where the evolution of the courtship trait is opposed by gene flow from an ancestral population, where alleles increasing the trait value are maintained at a low frequency. Such a scenario would apply if mate choice in the ancestral population were based on another (ancestral) courtship trait which is not effective in the new population for an environmental reason (e.g., carotene-based coloration in an environment poor in dietary carotene, or visual signals in murky water). Our results suggest that learning may be essential to allow a population that colonized a new environment to diverge in its courtship trait from the ancestral population despite continuing gene flow. On the other hand, the mean genotypic value of the courtship trait at equilibrium between local selection and gene flow decreases with increasing learning rate; as a result, with a high learning rate, the genetic assimilation of the courtship trait is thwarted (Fig. 6). Thus, at least under the scenario considered here, learning can act as a first step reducing gene flow to some degree, but would act against the evolution of complete genetic isolation, at least in the absence of other factors favoring the reduction of gene flow (e.g., ecologically-mediated divergent selection; Schluter and Conte, 2009).

The scenario assumed here – that males learn from encounters with females and gradually improve their courtship performance – requires that females are per-

sistent in their preference. Otherwise, by the time the males have learned, females are already mating at random. Thus, rather than on its absolute magnitude, the effect of learning on evolution depends on the relative value of the learning rate L and the parameter a describing how fast unmated females revert to random mating. Therefore, the learning rate which most strongly facilitates the evolution of the courtship trait is positively correlated with parameter a (see Fig. 2B). This is intuitive when one considers the extreme cases. If females always mate at random with the second male they encounter, only very fast learning, allowing males with genotypic value well below the mating threshold to reach the mating threshold in one step, would have a noticeable effect. At the other end of the spectrum, if females never accept males below the mating threshold, the learning rate that maximizes selection at the genotypic level would be very low – in such a case males with the highest innate trait values would be assured to obtain the majority of matings.

Our model has many parameters, and we only explored the effects of a few. We can offer some informed speculations about the effects of some of the remaining parameters. If the trait were affected by more loci with smaller effects (keeping the range of variability the same), the additive genetic variance of the trait would be reduced. More importantly, in the absence of learning the effectiveness of sexual selection depends on the rare recombinants that exceed the mating threshold while the mean genotypic value is still low. Such extreme recombinants would be even less frequent with more loci with smaller effects, thus increasing the importance of learning as a stepping-stone to the evolution of the novel courtship trait. We assumed that the innate expression of the courtship trait is affected by random developmental noise. An alternative assumption is that the courtship trait by the male is affected by an independent random error every time the male encounters a female. This would be equivalent to assuming a random component affects the female inspection and mating decision. Preliminary simulations (results not shown) indicate that these alternative assumptions have negligible effect on the results. Small population size should result in more pronounced genetic drift. This would increase the likelihood that the genotypic values in the population reach the vicinity of the mating threshold by drift, at which point sexual selection would become effective even without learning. However, a more likely effect of drift would be the loss of alleles increasing the courtship trait. Finally, a female-biased operational sex ratio

would result in a greater average number of encounters per male, thus giving them more opportunity to learn; it would thus be expected to have a similar effect as a smaller value of parameter a (and vice versa for a male-biased sex ratio).

Our model is tailored to a polygynous species where females mate only once and males contribute nothing but sperm. However, some of the qualitative conclusions may generalize to other mating systems. Assuming that females can mate multiple times while retaining other assumptions of the model would increase the number of opportunities for learning, similarly to a female-biased sex ratio. Thus, we would expect qualitatively similar results to those presented above, except that the evolutionary dynamics observed for a particular value of learning rate with singly-mating females would be expected for a lower learning rate if females mated multiply. However, the situation would be more complex than with female-biased sex ratio because with multiple mating the initial success of males that achieve matings early would be diluted by other males that mated with the same female later, in particular if last male sperm precedence was assumed. It is more difficult to extrapolate to species with paternal care, but one might speculate that instrumental learning of traits involved in courtship might facilitate the evolution of behaviors that indicate the potential partner's quality as a provider of such care, as well as facilitate the evolution of traits involved in soliciting extra pair matings. Finally, by symmetry, our model could be applied to evolution of female courtship traits in polyandrous species with reversed sex roles, such as black coucal (Andersson, 1995) or pipefish (Widemo, 2006).

The scenario we are proposing relies on the key assumption that males are actually able to develop more attractive courtship in response to behavioral feedback from females even if the feedback does not initially lead to mating. We are aware of two examples that support this assumption. First, male cowbirds (which, being nest parasites, cannot learn song from their father) develop a population-specific song by trial-and-error learning, relying on a behavioral response from females (wing flicking; West and King, 1988; Dohme et al., 2015). Second, when faced with a group of females of which only one is receptive, naïve *Drosophila* males gradually learn to focus their courtship effort on the receptive female (Hollis and Kawecki, 2014). This presumably occurs in response to behavioral cues from females, such as those reported by Dukas and Scott (2015); Verzijden et al. (2015) show that *Drosophila* males can learn to

associate an arbitrary trait with female receptivity. These studies suggest that males not only pay attention to behavioral cues from females, but that these cues can act as a reinforcer of courtship behavior. Our model, while admittedly simplistic, demonstrates that, at least in theory, such instrumental learning can be a key factor that mediates the evolution of novel courtship traits and divergence in courtship traits between populations.

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