

The impact of learning on sexual selection and speciation

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Learning is widespread in nature, occurring in most animal taxa and in several different ecological contexts and, thus, might play a key role in evolutionary processes. Here, we review the accumulating empirical evidence for the involvement of learning in mate choice and the consequences for sexual selection and reproductive isolation. We distinguish two broad categories: learned mate preferences and learned traits under mate selection (such as bird song). We point out that the context of learning, namely how and when learning takes place, often makes a crucial difference to the predicted evolutionary outcome. Factors causing biases in learning and when one should expect the evolution of learning itself are also explored.

Learning as a driving force in evolutionary change

It is now increasingly appreciated that several non-genetic mechanisms can influence evolutionary change (e.g., [1]), and among these are learned behaviors. Learning, which has been studied in depth in many species, is a common process involved in the development of behavior. Although this research field has long been separated from the study of genetic evolution, connections between these disciplines have recently received attention [2]. In particular, the number of studies connecting the development of behavior with studies of speciation and sexual selection has increased rapidly. Concurrently, theoretical developments are uncovering the effects of learned preferences and traits on the dynamics of evolution in these contexts.

We discern two broad categories of learned behavior directly affecting mate choice: learned behavior that affects preferences for mates, and learned traits that are the direct targets of mate choice. Therefore, we define learning here in the context of mate choice as a process that affects the development of preferences and behavior involved in mate choice or mate attraction, through exposure to stimuli that constitute the specific phenotypes or behavior of potential mates, conspecifics, or individuals of other species. Mere exposure to (in the case of imprinting), or interaction with (in the case of social or reinforced learning), these stimuli can change responses to the same or similar stimuli on future encounters. In this review, we focus on the effects of learning on mate choice and its consequences for sexual selection and speciation. Mate choice typically requires preferences of one sex for certain traits in the other; therefore, we examine both mate preference learning and learning of mating traits.

The study of the role of learning in the development of mate choice has a long track record that has provided insight into how widespread and diverse this phenomenon is. A summary of sexual imprinting and other forms of preference learning (including examples of each) is provided in Box 1. Unlike learned preferences, the learning of traits under sexual selection has mainly been shown in the song of oscine passerines (reviewed recently in several papers e.g., [3–5]). However, a few examples are emerging from other behaviors and taxa, such as courtship displays and human behavior (e.g., [6-9]). Learned behavior is challenging to demonstrate, because controlled rearing experiments are often necessary to be able to convincingly demonstrate learning. Therefore, we expect more examples of learned preferences and traits to accumulate as researchers look for this evidence more specifically.

The relationship between learned mate choice and phenotypic plasticity

Learning can be viewed as a form of phenotypic plasticity. Thus, key concepts from research in plasticity could be used in learning research to facilitate integration between the proximate research tradition on learning and evolutionary research terminology. The concept of reaction norms is central to quantitative genetics and phenotypic plasticity [10] and can be applied to mate choice. Specifically, we suggest that, in the case of mate choice, reaction norms become analogous to preference functions, which have been used traditionally to model preferences for male secondary sexual traits [11]. Mate preference functions quantify the mating response as a continuous function of variation in a quantitative male trait (i.e., a length of a tail), and can differ in linear slopes, curvature, or intercept [11] (Figure 2a). For instance, increasing the amount of the cue could result in a stronger mate response and increased propensity to mate (resulting in directional sexual selection). In Figure 2, we present the simplest scenario: when preference functions differ only in slope so that curvature

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Box 1. Evidence for learned mate preferences

Males and females of many species learn their mate preferences, and learning can take place throughout life. When learning occurs at an early stage of life, affecting pair formation at a much later stage in life, this is called sexual imprinting [65]. This requires a period of social interactions with, usually, closely related individuals (the imprinting set [13]), such as parents and siblings. Phenotypic traits, such as visual or olfactory ones, are learned from these models, resulting in the learner being able to discriminate its own species and sex (Figure 1g-h, main text). Prime examples of sexual imprinting come from birds, with over 100 species from 15 different orders demonstrating this behavior [32], even in brood parasitic species [66]. Recent studies have shown that other groups of vertebrates with parental care also show sexual imprinting, including some mammals (sheep and goats [67]) and fish (cichlids and sticklebacks [68-70]; Figure 1e, main text). Several species of poeciliid fish demonstrate learning while juveniles through exposure to phenotypes in their population (oblique or horizontal imprinting sets), which affects both within- and between-species mate preferences [59,71].

Mate preferences can also be learned when individuals are independent and mature. In many cases, individuals learn through experience with potential mates. For instance, female Syrian hamsters [72], male guppies [73], male fruit flies of at least three species [51,74], and *Calopteryx* damselfly females (Figure 1a,b, main text) [53] learn to discriminate against heterospecific mates after courtship interactions. In other species of damselflies with female-limited polymorphism, males learn to prefer the morph with which they had a successful mating experience [63,64].

In some cases, individuals need experience with variation in phenotypes before expressing a preference. For example, female field crickets and female treehoppers become choosier with experience, depending on the quality of the male with which they interacted [75–78]. Likewise, female wolf spiders from polymorphic populations prefer ornamented males, but only after experience with both ornamented and unornamented males [52,79].

Individuals can also learn from the experience of another individual with mates, and copy the mate choice of others [80], either by choosing that same individual (e.g., [18]), or generalizing from a particular trait of the male that other females choose [20].

and intercept can be ignored; however, our perspective can readily be extended to more complex scenarios. Thus, by thinking of preference functions as a type of reaction norm, the variation in mating cues between potential mates is viewed as a variable mate 'environment'. The traits could also vary between closely related (but interacting) species, and could be qualitative instead of quantitative.

However, different genotypes might respond differently to the same amount of cue, resulting in reaction norms with different slopes (blue lines, Figure 2a). This would indicate that there is genotype \times environment interaction (i.e., genetic variation in phenotypic plasticity) [12]. This situation could exist without any learned mate preferences if the slopes of these reaction norms reflected solely genetic variation among individuals of the sex that chooses (Figure 2a). However, these slopes could also change within individuals or genotypes (i.e., during ontogeny). When there is such an ontogenetic change in slope, learning can be said to occur (Figure 2b). In other words, through experience, a genotype can express different mate preference phenotypes during different ontogenetic life stages (i.e., in response to the mate environment). Thus, in the terminology of phenotypic plasticity, the effect of mate preference learning is to change the slope (or curvature) of the reaction norms within genotypes. We note that, as a result of learning, variation in preference functions between individuals can be introduced in later life stages even when such variation did not exist in earlier ones.

Theoretical predictions of the evolutionary consequences of learning during mate choice

The existence of preferences and traits that can be acquired or modified by learning can have consequences for both the action of sexual selection and the evolution of pre-mating isolation during speciation. Although these consequences have been investigated to some extent by mathematical models, such studies are relatively few in number. Learning is a multifaceted phenomenon in part because different cases vary in the segment of the population that individuals learn from (the generalizable concept of the 'imprinting set' [13]) or how this learning occurs, and in part because, as discussed above, both preferences and traits can be learned. Both factors can have profound effects on the predicted evolutionary consequences of learning. Although some tantalizing, but tentative, conclusions can be drawn from current theoretical studies, this area begs more thorough investigation.

Sexual selection

For the case of sexual selection per se, mathematical models that have investigated the consequences of learning have arrived at few generalities. Mating preferences acquired by parental imprinting, for example, have been found to stabilize sexual selection onto a specific trait phenotype in some situations [14,15], but can cause runaway sexual selection under other conditions, including when preferences are also affected by a directional bias ([14,16], see also [17]). Mate choice copying also has a variety of effects. In some cases, it directly increases the fitness of the chosen individual, such as in the ocellated wrasse (Symphodus ocellatus) and whitebelly damselfish (Amblyglyphidodon leucogaster), where the attraction of one female increases the likelihood of attracting more females [18,19]. This can lead to positive frequency-dependent selection on male traits and potentially trait fixation, for example when the copied preference is not for an individual male but generalized to males with similar traits to the male initially chosen [20]. However, models predict that, depending on whether females are influenced in similar or different ways by prior observations, mate choice copying can create anything from positive [21,22] to negative frequency dependence and, in some cases, can even lead to the rapid spread of a novel trait [21]. Therefore, the consequences of learning on sexual selection are expected to be specific to several biological factors, and might have to be investigated on a case-by-case basis.

Speciation

By contrast, for the case of speciation, theoretical studies indicate that it is possible to make some tentative but interesting generalities about the effects of learning based simply on knowledge of the imprinting set and whether learning affects preferences or traits (see Box 2 for empirical examples). When traits that act as mating cues are altered or acquired by learning, this can cause a disassociation between genotype and phenotype (the phenotype is



Figure 1. Recent experimental studies demonstrating mate preference learning. Preference learning has now been demonstrated in insects (a-c), amphibians (d), fish (e) and several species of birds (f-h). *Calopteryx splendens* females learn to distinguish between con- and heterospecific males based on the amount of wing melanin in males, differentiating between small wing spots [(a) *C. splendens*] or fully melanized wings {(b) *Calopteryx virgo* [53]}. (c) In the butterfly *Bicyclus anynana*, mate choice is based on the size of wing spots, and learning results in a receiver bias for exaggerated spots (A. Monteiro, unpublished data). (d) In poison dart frogs (*Dendrobates pumilio*) with maternal care, cross-fostered offspring imprint on the color morph of their foster parents. Such learned mate preferences might preserve the extensive color morph diversity of this species on Bocas del Toro, Panama (C. Richards Zawacki, unpublished data). (e) In maternal mouth-brooding cichlids from East African lakes [*Pundamilia nyererei* (red), *Pundamilia pundamilia* (blue), *Mbipia lutea* (yellow), and *Mbipia mbipi* (black)], cross-fostering between species has also revealed that imprinting on the foster mother affects adult mate preferences [69,70]. (f) A male zebra finch (*Taeniopygia guttata*) courting a female Bengalese Finch (*Lonchura striata*). Such heterospecific courtship has been observed after experimental cross-fostering of nestlings between these two species. Therefore, mate preferences in these finches are affected by parental imprinting on the foster parent [32]. (g-h) Similarly, when great tis (*Parus major*) are cross-fostered to blue tis (*Cyanistes caeruleus*), they prefer to mate with the species of the foster parent, copy their songs and alarm calls, treat them as their main competitors and copy their foraging niche [82,83,85]. Photographs reproduced with permission from: Erik Svensson (a,b,g-h); Antonia Monteiro (c); Corinne Richards Zawacki (d); Ole Seehausen (e); and Carel ten Cate (f).

essentially plastic). In cases where selection opposes divergence, such as stabilizing or positive frequency-dependent sexual selection in a uniform direction in allopatric populations, the relaxed selection on genotype caused by learning can facilitate divergence by genetic drift, enabling speciation [23]. However, when genetic divergence is driven by natural or sexual selection, such as during speciation with gene flow, this masking of the genotype by learning can inhibit speciation (e.g., [24,25]), even though it can promote phenotypic diversification in some circumstances [26,27].

Unlike learned traits, learned preferences are generally expected to promote speciation with gene flow (Box 3), and these effects can be profound. One of the principal impediments to the evolution of pre-mating isolation when there is gene flow is that the statistical associations (linkage disequilibrium) between distinct sets of preferences and traits can be broken by recombination, inhibiting divergence [28]. A special case in which this does not occur is self-referent phenotype matching, in which females, for example, simply mate with a male that matches their own phenotype (a 'one-allele' model sensu Felsenstein [28]). Maternal or paternal imprinting can mimic self-referent phenotype matching [29,30], thus generating assortative mating by a mechanism that cannot be broken by recombination because there are no separate alleles for different preferences. However, assortative mating is not generated when sexual imprinting is based upon non-parental individuals (i.e., is 'oblique' or 'horizontal'); such imprinting can create strong positive frequency dependence, eliminating variation in traits, and renders preferences effectively nonheritable. This prevents the associations between



Figure 2. Graphical models relating learned mate preferences to the concept of phenotypic plasticity, reaction norms, and genotype × environment interaction. (a) In a situation without learning, different genotypes within the same species can respond differentially towards the amount of a mating cue in terms of their mating propensity (willingness to mate: blue lines; aversion to mate: red line). The different slopes reveal genetic variation in mating propensity (genotype × environment interaction). (b) By contrast, mate preference reaction norms do change during the course of ontogeny when learning is involved. Here, a single genotype is shown when sexually inexperienced (green line) and when it might still be indifferent to the amount of mate recognition cue. During the course of the ontogeny, the same genotype encounters several prospective mates that vary in their amount of cue and suitability as a mate (mate quality or mate belong to the correct species). Therefore, the reaction norm slopes of different genotypes change as a result of positive or negative feedback, leading to increased preference (blue line) or increased aversion (red line) during sexual ontogeny.

preferences and traits that facilitate the buildup of divergence when there are high amounts of gene flow [30].

Biases

Learned preferences for traits often show some directionality [31,32] in that the preference deviates from the trait value of the model that was imprinted on. Such directionality might result in offspring that do not prefer the most common or average phenotype, but instead one that deviates from the population mean in a specific way (e.g., by having a more elaborate appearance or vocalization). Directionality of preferences in general can arise in different ways, varying from perceptual biases that develop independent of learning to those originating from the learning process itself [31]. Thus, although learning is not the only source of directionality in preference (i.e., the developmental origin can also be genetic), its study is crucial to a thorough understanding of this phenomenon and subsequent trait evolution.

An example of a directionality that results from a combination of a non-learned perceptual bias and a learned preference is found in Japanese quail (*Coturnix coturnix japonica*). Quail raised with a white adult with a few painted dots prefer mates of this type over wild-type mates, but prefer white mates having more dots than their model, independent of exposure to this type [33]. One can imagine that such perceptual biases could evolve when the trait indicates particular qualities. Another cause for directionality in a preference is that non-learned biases can direct what individuals will learn. For instance, a genetically

Box 2. Effects of sexual imprinting on reproductive isolation in nature

The classic demonstrations of how learning can affect mating preferences and mating cues come from laboratory studies of sexual imprinting [32] and song learning [81] in birds. However, how important is early learning for mating and speciation under natural conditions? Several examples demonstrate the power of this mechanism.

In an extensive field study, eggs were exchanged between great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) (Figure 1g,h, main text) breeding in nest boxes. This manipulation had far-reaching behavioral consequences. Cross-fostered great tits, in particular, preferred to mate with the foster species [82], copied its songs [83], developed a similar alarm call structure [84], treated it as competitor [84], and adopted the foraging niche of the foster species [85]. Such effects can last for life, illustrating how many traits that are crucial to survival and reproductive isolation depend on early learning.

Long-term field studies on Darwin's finches indicate the evolutionary consequences of cultural transmission of deviant songs and song preferences across generations. In these species, songs and song preferences act as powerful pre-mating barriers and many observations indicate that they are of crucial importance in speciation in this group [86]. For instance, an immigrant medium ground finch [87] with a morphology and song that deviated from the existing population on Daphne Major Island gave rise to a reproductively isolated new lineage in which females only mated with the males singing the song of their own lineage, thus providing the foundation for future speciation.

Reproductive isolation by novel songs is also thought to be the driving factor for speciation in indigo birds (*Vidua* spp.). In this group of brood parasitic finches, each species is linked to a particular host species. DNA studies show that host and parasite did not co-speciate, but that parasitic birds had speciated more recently [88]. Laboratory experiments show that parasite males raised by a novel host species copy the song of the new host. Females raised by this host prefer conspecific males singing the song of the new host and select the novel species as host for their eggs [66]. Field data show that some parasite males sing nontraditional host species songs [89], suggesting that speciation in indigo birds is driven by presumably accidental egg laying in nests of novel host species. This results in parasites reproductively tuned to mates reared by this host, while becoming reproductively isolated from their parental type at the same time.

Box 3. When does learning promote reproductive isolation versus outbreeding?

Depending on the underlying process of learning, experience with a certain phenotype could lead individuals to prefer familiar phenotypes (as in sexual imprinting) or to avoid familiar phenotypes in mates (as in learned aversion). Most of the research on learning and the development of conspecific mate preference has focused on imprinting. Positive assortative mating will be strengthened when imprinted phenotypes are more similar to the phenotype of an individual, leading individuals to select phenotypically similar mates [30]. Thus, assortative mating and conspecific mate preference can often result from imprinting on related individuals (although imprinting on parents appears to have more widespread effects than does imprinting on siblings [32,62,68,69]). However, when mate preferences are based on adult phenotypes randomly encountered in the population, learning does not contribute to conspecific preference or assortative mating [30,52,79]. Assortative mating can also result when individuals imprint on aspects of their breeding habitat, such as when brood parasites imprint on host song and prefer conspecifics raised by the same host species [88] or when individuals imprint on the odor of natal habitats and later return to these habitats to breed [90].

Under learned aversion, previously experienced phenotypes are avoided and novel phenotypes are preferred in mates. For instance,

mediated color preference stimulates naïve chicks to learn from models having this color [34]. However, a directional bias can also develop without a genetic component. Experiments on filial imprinting in chicks have shown that preferences for particular traits can themselves be induced by prior experiences even in a different modality [35].

Bias-guided learning can also affect the development of mating cues. Many songbirds, for instance, have a bias to preferentially learn conspecific songs, which is due to a perceptual sensitivity to syntactic or phonetic features of these songs [36].

Finally, directionality in preference can also result from the learning process itself. One example is 'peak shift' [31]. Learning to discriminate between two very similar stimuli can result in a skewed generalization gradient in which the strongest responses are given to stimuli more distinct from each other than the training stimuli. Experiments on zebra finches (Taeniopygia guttata) have shown that directional preferences in beak color and song might arise in this way and, hence, potentially drive the divergence of traits within and between species [37,38]. Evidence that this peak shift process occurs in the field comes from two Darwin finch species (Geospiza fortis and Geospiza scandens) on Daphne Island that increased the trill rate of their songs when another species, with a lower trill rate, colonized the island [39] (Box 2). Peak shift might be involved in other examples of reproductive character displacement, but its presence has not yet been tested explicitly.

The evolution of learning

Much of the understanding of the evolution of learning comes from empirical work in contexts other than mate choice, such as food finding. In this case, variable ecological environments are generally expected to promote the evolution of learning [15] and experimental evolution studies show that the ability to learn is heritable [40] and responds to selection [41], resulting in selection lines with individuals that learn faster and have better memory retention.

In line with this work on learning and food finding, mathematical models have confirmed that learning can female guppies prefer unfamiliar male color patterns [91] and female mice (Mus musculus domesticus) learn to avoid sibling major histocompatibility complex (MHC) genotypes [92]. Learned aversion has been proposed to promote outbreeding because preferences for novel mates should increase gene flow between diverging populations. However, if there is selection for an optimal level of outbreeding, then individuals might prefer mates that are not identical to themselves (and thus avoid mating with kin), but reject mates that are too dissimilar (such as members of other populations) [93]. Such optimal outbreeding preferences can arise through learning [94] but is unclear whether they are a byproduct of imprinting or the result of additional learning processes. One form of learned aversion, which appears to involve a separate process, occurs when individuals learn to avoid heterospecifics during courtship due to negative experiences, such as rejection by heterospecific females or aggression received from males [51,53,72-74,95,96]. This learned aversion of heterospecifics might contribute to isolation when diverging species come into secondary contact [57]. Furthermore, learned heterospecific aversion seems likely to have different consequences compared with imprinted preferences for the evolution and maintenance of reproductive isolation, but additional theoretical and empirical work is needed.

evolve in the contexts of sexual selection and speciation, although with limitations. Models of trait learning, which have generally considered learned bird song, have found factors that both facilitate and inhibit song production learning [25,42,43]. The evolution of learned preferences currently appears more straightforward than does the evolution of learned traits. A gene for a learned preference is expected to evolve when it either lowers mating costs [44] or is favored by sufficiently strong indirect selection (e.g., [45]). In the latter case, the 'imprinting set' has been identified as a particularly crucial factor in determining whether a gene for a specific learned preference will evolve [13]. If this set includes a high frequency of individuals carrying a trait with high fitness, positive genetic associations will form between the successful trait and the gene for the imprinting strategy, leading to the spread of the latter [13,45]. Finally, because parental imprinting, as discussed above, is an excellent proxy for phenotype matching in models of speciation [30], it is expected to evolve particularly easily in the scenario of speciation with gene flow (e.g., [28]), although, to our knowledge, this has not yet been specifically modeled or observed.

These forces promoting the evolution of learning can be countered by costs, which will affect whether learning will evolve. In studies of learned food finding, the evolved ability to learn comes at a cost in traits such as larval competitive ability [41] or fecundity [46]. Also, the act of learning itself comes at a cost, affecting fecundity and longevity in several studies [46–48]. If the costs of learning are high, the ability to learn would be expected to decline. In the terminology of phenotypic plasticity, the slope of the reaction norm would be less susceptible to changes through experience [i.e., the behavior would tend to become canalized (e.g., [45])]. This might have occurred, for example, in Trinidadian guppies (*Poecilia reticulata*), where populations sympatric with a congener without experience discriminate against heterospecifics, whereas allopatric populations must learn this discrimination through courtship experience [49].

There are currently no published studies on the experimental evolution of mate preference learning or trait learning. However, there are several social and ecological conditions that might affect the evolution of learned mate choice. As discussed above, a variable environment can lead to the evolution of learning [15], which might extend to variable social environments promoting learned conspecific mate preference. Demography influences encounter rates between males and females, and the costs and benefits of mate choice. Thus, temporal and spatial variation in factors such as population density, relative densities of sympatric closely related species, and operational sex ratio, could be important determinants of whether mate preference learning evolves. For example, a low probability of encountering heterospecifics during crucial periods for imprinting reduces the possibility of misimprinting and, thus, learned preference could be favored under such conditions (Box 3).

The evolution of learning can be affected by life history and social behavior

It seems logical that particular life-history traits might promote the evolution of learned conspecific mate recognition and preference. Particular traits that come to mind are longevity, iteroparity, parental care, and sociality. This area is in particular need of further research because it is possible to speculate about several directions in which these effects could occur. For example, long-lived species might have more opportunities for both learning to occur and the benefits of learning to be realized. Although learning is not confined to long-lived species, learning in insects and other arthropods is often in the context of foraging, route finding, or oviposition (e.g., [40,50]), but occasionally occurs in mating [51–53]. Second, iteroparous species and those that mate multiple times during a breeding season can learn from early breeding experience to guide subsequent courtship and choice (e.g., [54]). Although mate choice in short-lived species and semelparous species might be under strong selection, given the very few chances to 'get it right', mechanisms other than learning might be more likely to evolve to guide those choices. Variation in ecological and social factors could affect at what life stage learning evolves (i.e., imprinting or learning at a later life stage), what kind of preference results from the learning (i.e., attraction or avoidance), and what trait(s) learning is based upon. Third, the degree of sociality influences the extent of interaction with conspecifics and of sensitivity to social cues, and might also favor the learning of social partner preferences. This is not to say that asocial species cannot learn mate preferences and certainly some do (e.g., [44]), but rather that learning might be more widespread or more pronounced in social species.

A particular way in which social behavior can influence the evolution of learned mate preferences is that learning in other behavioral contexts could predispose taxa to evolve learned conspecific recognition and preference. Learning in one context is known to transfer to other contexts under some conditions and might be facilitated if learning is genetically correlated with the learned traits [55]. Transfer could arise because the propensity to learn is in place, as is the neural machinery to support such learning, which might reduce the cost of learning mate preferences. The extent to which other contexts share features with mate choice might increase the likelihood of transfer. Two contexts seem particularly likely to play this role: social (observational) learning [56] and learned recognition of individuals or group members [57].

Social learning of food finding, food processing, parental care, or predator avoidance requires that an individual attends to the behavior of others and retains memory of those actions to guide the subsequent behavior of the learner [58]. This close attention to the phenotype and behavior of demonstrators, coupled with the memory required for social learning, might predispose taxa to learn mate preferences. Mating is a social interaction, and mate choice can demand assessment of several phenotypic traits, including complex courtship behavior [59]. Moreover, comparison of potential mates requires memory [60].

Learned recognition of individuals or group members also seems likely to influence learned conspecific recognition. The essential three components of recognition systems will be in place and extensible to the mating context: (i) cues that indicate identity; (ii) the ability to discriminate among these cues; and (iii) behavioral responses (i.e., preferences) based on that discrimination. For example, social partner preferences are learned in some species, and this has been shown to influence subsequent mate preferences [61,62].

Sex differences in social structure or in the different roles that the sexes take in mating could also influence the opportunity or propensity for learning. For instance, the searching sex might be more likely to form a 'search image' of a preferred phenotype, whereas the non-searching sex might learn to discriminate among phenotypes as members of the other sex approach them to mate. Although few studies have measured the learning propensities of both sexes within single species, forms of learning do seem to vary among the sexes in some taxa [53,62–64]; however, sex roles during mate choice could also affect whether and how learned preferences are expressed [32].

A broader outlook

Evidence is now accumulating that learned mate preferences and learned display traits can contribute to sexual selection, the evolution of reproductive isolation (Boxes 2 and 3), population divergence, and sexual conflict (Box 4). That learned mate choice behavior can cause strong and dynamic effects on population genetic patterns is clear. However, it is currently unclear how these effects differ from those of genetically inherited traits: do they promote faster evolution, or do they lead to evolution in different directions or through different pathways? These are fundamental evolutionary questions that require major advances in at least three lines of research. We have focused below on preference learning because that provides the broadest scope, but it would also be useful to know the extent to which display traits, other than bird song, are learned.

First, greater understanding is needed about which factors facilitate the evolution of learned preferences. Can learning evolve, under what circumstances, and what pleiotropic effects are there of learning? For instance, one basic question currently unanswered is; how much genetic variation is present in mate preference learning? How

Box 4. Sexual conflict and learning in damselflies

The evolutionary consequences of learned preferences can be influenced by the extent of male mating harassment and the magnitude of sexual conflict. For instance, when males learn to recognize certain female phenotypes and perceive them as attractive, these male preferences can be costly to the preferred females by lowering fecundity [97] or increasing mortality due to excessive male mating harassment. This might even skew sex ratio in the population. Females with the preferred phenotypes would then be selected against, and decrease in frequency in the population.

The victims of male mating harassment could change rapidly if males switch their 'search images' towards the female phenotypes that are currently common and, hence, easy to find. Rapid switching of male search images is facilitated if males have learned mate preferences, for which there is now some evidence from damselflies of the genus *lschnura* [64] (Figure la–c,f). Rapidly changing male mate preferences will then lead to a 'chase' of the common female phenotypes [63,64,98], particularly at high densities [97], through negative frequency-dependent selection.

Field studies of male mating harassment (clasping attempts) and estimation of fecundities across populations with different morph frequencies jointly indicate that the degree of male mating harassment is both morph specific and density dependent (Figure Id). In *Ischnura elegans*, the degree of male mating harassment increases faster with increasing density for gynochrome females than for androchrome females, leading to greater morph differences at higher densities, compared with lower densities (Figure Id) [97]. Female fecundities are also negatively frequency dependent, which maintains the morphs over evolutionary time, based on population genetic simulation modeling (Figure Ie) [98]. Negative frequency-dependent selection can interact with the different temperature tolerances of the different female morphs, causing a strong geographic cline in morph frequencies in *Ischnura senegalensis* from south to north in Japan, with the androchrome female morph being more common in the north [99] (Figure If).



Figure I. In several species of damselfly in the genus *lschnura*, there are either three **[(a-c)** *lschnura elegans*] or two (*lschnura senegalensis*) heritable female morphs that coexist in local populations. One of the female morphs is typically male colored (blue) and is considered to be a male mimic ['androchrome' females; **(c)**], whereas the other female morph(s) differs from males in both coloration and patterning (a,b; often called 'gynochrome' females). **(d)** Density-dependent mating harassment on androchrome females (filled circles) and gynochrome females (open triangles). **(e)** Simulations of negative frequency-dependent selection on morphs: different colors are frequencies of the different morphs in *I. elegans*, with blue denoting androchrome females). **(f)** *I. senegalensis* shows a strong geographic cline in morph frequencies from south to north in Japan, with the androchrome female morph becoming more common in the north. Photographs reproduced with permission from T. Gosden (d), (e) and Y. Takahashi (f).

much does learning in other contexts affect mate preference learning, or trait learning? What costs are associated with mate preference learning ability, are they similar to food preference learning or to oviposition substrate preference learning? One promising future approach to address such questions is to use artificial selection to evolve learning in the context of mate choice. Likewise, the genetic architecture of learning needs to be investigated. If genes affecting preference learning are physically linked to genes for traits, this could protect linkage disequilibrium between the two, potentially facilitating the evolution of learned preferences. Such linkage could also have important implication for the speciation process [28].

Second, to predict the direction of evolution, there should be a better understanding of the preference functions individuals acquire through learning. For instance, what processes give rise to peak shift, or more generally, directional deviation of preferences from the model on which the preference was based? Are there differences in what or how each sex learns about mating traits? Is there a difference in learning from within- and between-species interactions? What kinds of interaction lead to a learned preference or a learned aversion? To answer most of these questions, more information needs to be gathered on the shape of preference functions in naïve versus experienced individuals.

Third, we suggest investigations into the ecological factors affecting the evolution of mate preference learning. To this end, species with populations that vary in the degree of mate preference learning would allow for interesting comparative studies. For instance, by comparing such populations, one could estimate the tradeoff between the time needed for learning versus other fitness-related traits, such as time to mate and time invested in mate searching. Another interesting comparison would be to ask what ecological and social contexts are associated with the evolution of learning. For instance, does population density, living in a marginal habitat, or living at the geographical range limit of a species affect the evolution of learning? Cumulatively, such data would allow a comprehensive understanding of how learning and other non-genetically inherited traits affect evolution.

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References

- 1 Danchin, E. et al. (2011) Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. Nat. Rev. Genet. 12, 475–486
- 2 Laland, K.N. et al. (2011) Cause and effect in biology revisited: is Mayr's proximate-ultimate dichotomy still useful? Science 334, 1512–1516
- 3 Beecher, M.D. and Brenowitz, E.A. (2005) Functional aspects of song learning in songbirds. *Trends Ecol. Evol.* 20, 143–149
- 4 Byers, B.E. and Kroodsma, D.E. (2009) Female mate choice and songbird song repertoires. *Anim. Behav.* 77, 13-22
- 5 Soma, M. and Zsolt Garamszegi, L. (2011) Rethinking birdsong evolution: meta-analysis of the relationship between song complexity and reproductive success. *Behav. Ecol.* 22, 363-371
- 6 Aronsson, H. et al. (2011) Parental influences on sexual preferences: the case of attraction to smoking. J. Evol. Psychol. 9, 21–41
- 7 Janik, V.M. and Slater, P.J.B. (2000) The different roles of social learning in vocal communication. Anim. Behav. 60, 1-11
- 8 Madden, J.R. (2008) Do bowerbirds exhibit cultures? Anim. Cogn. 11, 1–12
- 9 Williams, H. (2001) Choreography of song, dance and beak movements in the zebra finch (*Taeniopygia guttata*). J. Exp. Biol. 204, 3497–3506
- 10 Sultan, S.E. and Spencer, H.G. (2002) Metapopulation structure favors plasticity over local adaptation. Am. Nat. 160, 271–283
- 11 Lande, R. (1981) Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. U.S.A: Biol. Sci. 78, 3721–3725
- 12 Via, S. and Lande, R. (1985) Genotype–environment interaction and the evolution of phenotypic plasticity. *Evolution* 39, 505–522
- 13 Tramm, N.A. and Servedio, M.R. (2008) Evolution of mate-choice imprinting: competing strategies. *Evolution* 62, 1991–2003
- 14 Aoki, K. et al. (2001) Models of sexual selection on a quantitative genetic trait when preference is acquired by sexual imprinting. Evolution 55, 25–32

- 15 Laland, K.N. (1994) On the evolutionary consequences of sexual imprinting. *Evolution* 48, 477–489
- 16 Ihara, Y. et al. (2003) Runaway sexual selection with paternal transmission of the male trait and gene-culture determination of the female preference. *Theor. Popul. Biol.* 63, 53–62
- 17 Laland, K.N. (1994) Sexual selection with a culturally transmitted mating preference. *Theor. Popul. Biol.* 45, 1–15
- 18 Alonzo, S.H. (2008) Female mate choice copying affects sexual selection in wild populations of the ocellated wrasse. Anim. Behav. 75, 1715–1723
- 19 Goulet, D. and Goulet, T.L. (2006) Nonindependent mating in a coral reef damselfish: evidence of mate choice copying in the wild. *Behav. Ecol.* 17, 998–1003
- 20 Godin, J.G.J. et al. (2005) Social influences on female mate choice in the guppy, *Poecilia reticulata*: generalized and repeatable trait-copying behaviour. *Anim. Behav.* 69, 999–1005
- 21 Agrawal, A.F. (2001) The evolutionary consequences of mate copying on male traits. *Behav. Ecol. Sociobiol.* 51, 33–40
- 22 Kirkpatrick, M. and Dugatkin, L.A. (1994) Sexual selection and the evolutionary effects of copying mate choice. *Behav. Ecol. Sociobiol.* 34, 443–449
- 23 Lachlan, R.F. and Servedio, M.R. (2004) Song learning accelerates allopatric speciation. *Evolution* 58, 2049–2063
- 24 Olofsson, H. *et al.* (2011) Can reinforcement occur with a learned trait? *Evolution* 65, 1827–2132
- 25 Olofsson, H. and Servedio, M.R. (2008) Sympatry affects the evolution of genetic versus cultural determination of song. *Behav. Ecol.* 19, 594–604
- 26 Ellers, J. and Slabbekoorn, H. (2003) Song divergence and male dispersal among bird populations: a spatially explicit model testing the role of vocal learning. *Anim. Behav.* 65, 671–681
- 27 Bailey, N.W. and Moore, A.J. (2012) Runaway sexual selection without genetic correlations: social environments and flexible mate choice initiate and enhance the Fisher process. *Evolution* http://dx.doi.org/ 10.1111/j.1558-5646.2012.01647.x
- 28 Felsenstein, J. (1981) Skepticism towards Santa Rosalia, or why are there so few kinds of animals. *Evolution* 35, 124–138
- 29 Servedio, M.R. *et al.* (2009) Reinforcement and learning. *Evol. Ecol.* 23, 109–123
- 30 Verzijden, M.N. et al. (2005) Female mate-choice behavior and sympatric speciation. Evolution 59, 2097–2108
- 31 ten Cate, C. and Rowe, C. (2007) Biases in signal evolution: learning makes a difference. *Trends Ecol. Evol.* 22, 380–387
- 32 ten Cate, C. and Vos, D.R. (1999) Sexual imprinting and evolutionary processes in birds: a reassessment. In Advances in the Study of Behavior (vol. 28) (Slater, P.J.B. et al., eds), In pp. 1–31, Academic Press
- 33 ten Cate, C. and Bateson, P. (1989) Sexual imprinting and a preference for supernormal partners in Japanese quail. Anim. Behav. 38, 356–357
- 34 van Kampen, H.S. and de Vos, G.J. (1991) Learning about the shape of an imprinting object varies with its color. Anim. Behav. 42, 328-329
- 35 Lickliter, R. and Stoumbos, J. (1991) Enhanced prenatal auritory experience facilitates species-specific visual responsiveness in bobwhite quail chicks (*Colinus virginianus*). J. Comp. Psychol. 105, 89–94
- 36 Marler, P. and Peters, S. (1988) The role of song phonology and syntax in vocal learning preferences in the song sparrow, *Melospiza melodia*. *Ethology* 77, 125–149
- 37 ten Cate, C. et al. (2006) Sexual imprinting can induce sexual preferences for exaggerated parental traits. Curr. Biol. 16, 1128–1132
- 38 Verzijden, M.N. et al. (2007) Song discrimination learning in zebra finches induces highly divergent responses to novel songs. Proc. R. Soc. B: Biol. Sci. 274, 295–301
- 39 Grant, B.R. and Grant, P.R. (2010) Songs of Darwin's finches diverge when a new species enters the community. *Proc. Natl. Acad. Sci. U.S.A.* 107, 20156–20163
- 40 Snell-Rood, E.C. and Papaj, D.R. (2009) Patterns of phenotypic plasticity in common and rare environments: a study of host use and color learning in the cabbage white butterfly *Pieris rapae*. *Am. Nat.* 173, 615–631
- 41 Mery, F. and Kawecki, T.J. (2003) A fitness cost of learning ability in Drosophila melanogaster. Proc. R. Soc. Lond. Ser. B: Biol. Sci. 270, 2465–2469
- 42 Aoki, K. (1989) A sexual-selection model for the evolution of imitative learning of song in polygynous birds. Am. Nat. 134, 599–612

Review

- 43 Lachlan, R.F. and Feldman, M.W. (2003) Evolution of cultural communication systems: the coevolution of cultural signals and genes encoding learning preferences. J. Evol. Biol. 16, 1084–1095
- 44 Pruett-Jones, S. (1992) Independent versus nonindependent mate choice – do females copy each other. Am. Nat. 140, 1000–1009
- 45 Servedio, M.R. and Kirkpatrick, M. (1996) The evolution of mate choice copying by indirect selection. Am. Nat. 148, 848–867
- 46 Snell-Rood, E.C. et al. (2011) Reproductive tradeoffs of learning in a butterfly. Behav. Ecol. 22, 291–302
- 47 Mery, F. and Kawecki, T.J. (2004) An operating cost of learning in Drosophila melanogaster. Anim. Behav. 68, 589–598
- 48 Mery, F. and Kawecki, T.J. (2005) A cost of long-term memory in Drosophila. Science 308, 1148
- 49 Magurran, A.E. and Ramnarine, I.W. (2005) Evolution of mate discrimination in a fish. Curr. Biol. 15, R867-R868
- 50 Leadbeater, E. and Chittka, L. (2007) Social learning in insects from miniature brains to consensus building. *Curr. Biol.* 17, R703–R713
- 51 Dukas, R. (2009) Dynamics of learning in the context of courtship in Drosophila persimilis and D. pseudoobscura. Anim. Behav. 77, 253–259
- 52 Hebets, E.A. (2003) Subadult experience influences adult mate choice in an arthropod: exposed female wolf spiders prefer males of a familiar phenotype. Proc. Natl. Acad. Sci. U.S.A. 100, 13390–13395
- 53 Svensson, E.I. *et al.* (2010) A role for learning in population divergence of mate preferences. *Evolution* 64, 3101–3113
- 54 Moody, A.T. et al. (2005) Divorce in common murres (Uria aalge): relationship to parental quality. Behav. Ecol. Sociobiol. 57, 224–230
- 55 Mery, F. et al. (2007) Experimental evolution of olfactory memory in Drosophila melanogaster. Physiol. Biochem. Zool. 80, 399–405
- 56 Swaney, W. et al. (2001) Familiarity facilitates social learning of foraging behaviour in the guppy. Anim. Behav. 62, 591–598
- 57 Irwin, D.E. and Price, T. (1999) Sexual imprinting, learning and speciation. *Heredity* 82, 347–354
- 58 Shettleworth, S.J. (ed.) (2010) Cognition, Evolution and Behavior, Oxford University Press
- 59 Verzijden, M.N. and Rosenthal, G.G. (2011) Effects of sensory modality on learned mate preferences in female swordtails. *Anim. Behav.* 82, 557–562
- 60 Bailey, N.W. and Zuk, M. (2009) Field crickets change mating preferences using remembered social information. *Biology Letters* 5, 449–451
- 61 Kozak, G.M. and Boughman, J.W. (2008) Experience influences shoal member preference in a species pair of sticklebacks. *Behav. Ecol.* 19, 667–676
- 62 Kozak, G.M. and Boughman, J.W. (2009) Learned conspecific mate preference in a species pair of sticklebacks. *Behav. Ecol.* 20, 1282–1288
- 63 Fincke, O.M. et al. (2007) Lack of innate preference for morph and species identity in mate-searching *Enallagma* damselflies. *Behav. Ecol. Sociobiol.* 61, 1121–1131
- 64 Takahashi, Y. and Watanabe, M. (2010) Mating experience affecting male discrimination between sexes and female morphs in *Ischneura senegalensis* (Rambur) (Zygoptera: Coenagrionidae). Odonatologica 39, 47–56
- 65 Immelman, K. (1975) Ecological significance of imprinting and early learning. Annu. Rev. Ecol. Syst. 6, 15–37
- 66 Payne, R.B. et al. (2000) Imprinting and the origin of parasite-host species associations in brood-parasitic indigobirds, Vidua chalybeata. Anim. Behav. 59, 69–81
- 67 Owens, I.P.F. et al. (1999) Sexual selection, speciation and imprinting: separating the sheep from the goats. Trends Ecol. Evol. 14, 131–132
- 68 Kozak, G.M. et al. (2011) Sexual imprinting on ecologically divergent traits leads to sexual isolation in sticklebacks. Proc. R. Soc. B: Biol. Sci. 278, 2604–2610
- 69 Verzijden, M.N. et al. (2008) Females learn from mothers and males learn from others. The effect of mother and siblings on the development of female mate preferences and male aggression biases in Lake Victoria cichlids, genus Mbipia. Behav. Ecol. Sociobiol. 62, 1359–1368
- 70 Verzijden, M.N. and ten Cate, C. (2007) Early learning influences species assortative mating preferences in Lake Victoria cichlid fish. *Biol. Lett.* 3, 134–136
- 71 Walling, C.A. et al. (2008) Experience-induced preference for shortsworded males in the green swordtail, Xiphophorus helleri. Anim. Behav. 76, 271–276

- 72 delBarco-Trillo, J. et al. (2010) Adult female hamsters avoid interspecific mating after exposure to heterospecific males. Behav. Ecol. Sociobiol. 64, 1247–1253
- 73 Magurran, A.E. and Ramnarine, I.W. (2004) Learned mate recognition and reproductive isolation in guppies. *Anim. Behav.* 67, 1077–1082
- 74 Dukas, R. (2004) Male fruit flies learn to avoid interspecific courtship. Behav. Ecol. 15, 695–698
- 75 Bailey, N.W. and Zuk, M. (2008) Acoustic experience shapes female mate choice in field crickets. Proc. R. Soc. B: Biol. Sci. 275, 2645–2650
- 76 Fowler-Finn, K.D. and Rodriguez, R.L. (2012) Experience-mediated plasticity in mate preferences: mating assurance in a variable environment. *Evolution* 66, 459–468
- 77 Judge, K.A. (2010) Female social experience affects the shape of sexual selection on males. Evol. Ecol. Res. 12, 389–402
- 78 Rebar, D. et al. (2011) Mating experience in field crickets modifies pre- and postcopulatory female choice in parallel. Behav. Ecol. 22, 303–309
- 79 Hebets, E.A. and Vink, C.J. (2007) Experience leads to preference: experienced females prefer brush-legged males in a population of syntopic wolf spiders. *Behav. Ecol.* 18, 1010–1020
- 80 Vakirtzis, A. (2011) Mate choice copying and nonindependent mate choice: a critical review. Ann. Zool. Fennici 48, 91–107
- 81 Marler, P. and Tamura, M. (1964) Culturally transmitted patterns of vocal behavior in sparrows. *Science* 146, 1483–1486
- 82 Slagsvold, T. et al. (2002) Mate choice and imprinting in birds studied by cross-fostering in the wild. Proc. R. Soc. Lond. Ser. B: Biol. Sci. 269, 1449–1455
- 83 Johannessen, L.E. et al. (2006) Effects of social rearing conditions on song structure and repertoire size: experimental evidence from the field. Anim. Behav. 72, 83–95
- 84 Slagsvold, T. and Hansen, B.T. (2001) Sexual imprinting and the origin of obligate brood parasitism in birds. Am. Nat. 158, 354–367
- 85 Slagsvold, T. and Wiebe, K.L. (2007) Learning the ecological niche. Proc. R. Soc. B: Biol. Sci. 274, 19–23
- 86 Grant, P.R. and Grant, B.R. (1997) Genetics and the origin of bird species. Proc. Natl. Acad. Sci. U.S.A. 94, 7768–7775
- 87 Grant, P.R. and Grant, B.R. (2009) The secondary contact phase of allopatric speciation in Darwin's finches. *Proc. Natl. Acad. Sci. U.S.A.* 106, 20141–20148
- 88 Sorenson, M.D. et al. (2003) Speciation by host switch in brood parasitic indigobirds. Nature 424, 928–931
- 89 Payne, R.B. et al. (2005) Song mimicry of Black-bellied Firefinch Lagonosticta rara and other finches by the brood-parasitic Cameroon Indigobird Vidua camerunensis in West Africa. Ibis 147, 130–143
- 90 Hasler, T.D. and Schotz, A.T., eds (1983) Olfactory Imprinting and Homing in Salmon: Investigations into the Mechanism of the Imprinting Process, Springer-Verlag
- 91 Hughes, K.A. et al. (1999) Familiarity leads to female mate preference for novel males in the guppy, *Poecilia reticulata*. Anim. Behav. 58, 907–916
- 92 Penn, D. and Potts, W. (1998) MHC-disassortative mating preferences reversed by cross-fostering. Proc. R. Soc. Lond. Ser. B: Biol. Sci. 265, 1299–1306
- 93 Bateson, P. (1978) Sexual imprinting and optimal outbreeding. Nature 273, 659–660
- 94 Bateson, P. (1980) Optimal outbreeding and the development of sexual preferences in Japanese quail. J. Comp. Ethol. 53, 231–244
- 95 Izzo, A.S. and Gray, D.A. (2011) Heterospecific courtship and sequential mate choice in sister species of field crickets. *Anim. Behav.* 81, 259–264
- 96 Kujtan, L. and Dukas, R. (2009) Learning magnifies individual variation in heterospecific mating propensity. Anim. Behav. 78, 549-554
- 97 Gosden, T.P. and Svensson, E.I. (2009) Density-dependent male mating harassment, female resistance, and male mimicry. Am. Nat. 173, 709-721
- 98 Svensson, E.I. et al. (2005) Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. Am. Nat. 165, 567–576
- 99 Takahashi, Y. *et al.* (2011) A geographic cline induced by negative frequency-dependent selection. *BMC Evol. Biol.* 11, 256