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# Mate Choice and Learning

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## Introduction

While an individual's genetic framework is a major contributor in determining its eventual mate choice, the role of the environment in further influencing mating decisions has long been recognized. Animals gather information from the environment throughout life, and in some cases, may apply this information to increase their odds of obtaining a high-quality mate. In short, these individuals learn. Moreover, such learning can have a social component. "Social learning" is a general term that describes any learning based on observing, interacting with, and/or imitating others in a social context. Social learning can transmit information vertically, generation to generation (e.g., parent to offspring) and/or horizontally, within a generation (as individual to individual). This form of information transfer is generally referred to as "cultural transmission." This entry will focus on social learning that relates to mate choice – mate-choice learning.

Mate-choice learning can be separated into two broad categories: learning based on personal experiences with others (referred to as "private" or "personal information") or learning that results from the observation of others (referred to as "public information"). Learning from private experiences can occur at the juvenile or adult stage and may include encounters with conspecifics or heterospecifics, same sex or opposite-sex individuals (Figure 1). Mate-choice imprinting, for example, demonstrates how an early experience based on private information shapes subsequent mate choice. Conversely, public information refers to any information gained through the observations of other individual's experiences. An example of the use of public information is mate-choice copying, for example, when a female mimics the mating decision of another female in the population. Mate choice that is influenced by private information is sometimes termed "independent mate choice," whereas mate choice based on public information is "nonindependent mate choice."

Mate-choice learning, whether it is through the acquisition of private or public information, balances various costs and benefits. For example, the process of learning itself can be costly, a topic covered in depth elsewhere. Additionally, costs can come in the form of imprinting on the wrong species (which could lead to reduced fitness), or from copying another individual that has chosen poorly itself. Nonetheless, the prevalence of mate-choice learning across taxonomic groups suggests that there are significant benefits associated with mate-

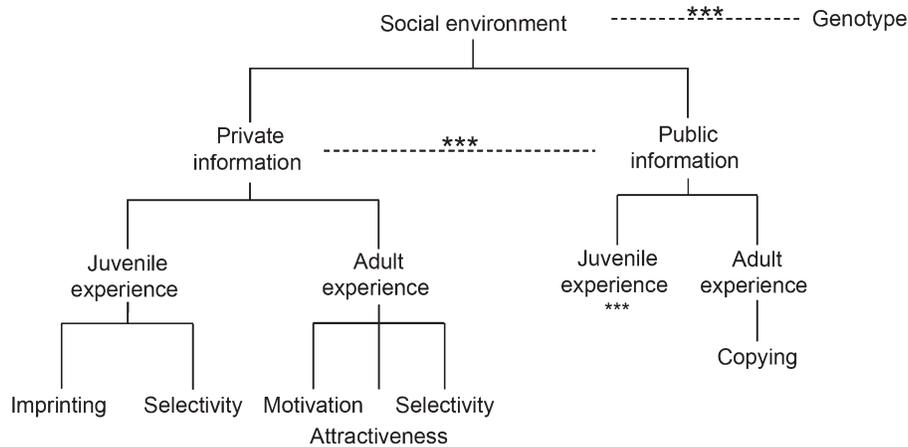
choice learning. For example, the use of public information relieves an individual from personally gathering information and could minimize costs typically associated with mate assessment such as exposure to predators or decreased time devoted to other important activities such as foraging. Mate-choice learning more generally permits flexibility in mate choice, which could be extremely important in a changing environment. In the following text, examples of different forms of mate-choice learning will be provided and the state of research in this area summarized.

## Private (Personal) Information

### *Juvenile Experience: Mate-Choice Imprinting*

"Mate-choice imprinting" refers to the learning process, or processes, by which young individuals acquire sexual preferences based on their observation of adults. Several specific forms of imprinting exist and the general tenet was first described by Douglas Spalding in the nineteenth century as he recounted his observations of newly hatched chicks following random moving objects. Despite its early description, however, the notion of imprinting was not popularized until the 1930s by the pioneering work of the Nobel Prize winning Austrian ethologist, Konrad Lorenz. Similar to other forms of imprinting (e.g., filial imprinting), sexual imprinting, or mate-choice imprinting, typically takes place during a sensitive period early in life. Historically, it has most frequently been observed in species with parental care, where the young use the parent of the opposite sex as the model upon which they base their future mating preferences. This kind of early mate-choice imprinting is thought to function to ensure conspecific matings, enabling individuals to avoid presumably costly heterospecific matings. Nonetheless, it is now clear that mate-choice imprinting is not always restricted to an early sensitive period and that preferences often continue to be modified throughout development.

Crossfostering experiments are one of the primary means by which scientists study early mate-choice imprinting and such studies are most easily, and frequently, conducted with birds. In crossfostering experiments, offspring are raised by parents of either another phenotype (e.g., a different color morph) or another species and, subsequently, their adult mate choice is examined. Using crossfostering experiments, mate-choice imprinting has been demonstrated in numerous bird species includ-



**Figure 1.** Mate-choice learning as influenced by social environment. This diagram depicts the various sources of social information that can impact mate-choice learning; the various life stages during which learning might be important; and some of the documented outcomes of mate-choice learning. Sections marked with “\*\*\*” indicate topics for which research is lacking or nonexistent, and we suggest that these might be potentially fruitful areas for future focus.

ing, but not confined to snow geese, zebra finches, Bengalese finches, great tits, blue tits, and red jungle fowl. In mammals, reciprocal crossfostering of sheep and goats has demonstrated a role of maternal imprinting on subsequent sexual preferences. Similarly, in Lake Victoria fishes, females of some species appear to imprint on the phenotype of their mother. Crossfostering experiments supporting a process of mate-choice imprinting are prevalent, yet studies do exist for which such early experiences have not influenced adult mate choice—raising interesting questions about species-level differences in the potential for, and importance of, mate-choice learning.

Traditional examples of mate-choice imprinting, as outlined earlier, are often restricted to species in which young spend significant time with their parents, thus, enabling parental imprinting (either paternal or maternal). However, mate-choice learning may also be prevalent in species that lack parental care, yet still have significant exposure to other conspecifics. For example, female wolf spiders are known to choose to mate with mature males of a phenotype with which they had experience as a subadult. This type of imprinting is referred to as “oblique imprinting”—imprinting on a nonparental adult. In another example of oblique imprinting, damselfly males alter their preference of female morphs based upon prior experience—males raised in the absence of females show no preference, while those raised with one female form subsequently exhibited a preference for females of that form. Planthoppers have also been shown to exhibit a learned preference for conspecifics. Finally, in humans for whom arranged marriages are the norm, the experiences young women have outside the traditional family environment, including exposure to outside media and participation in youth groups, influence their involvement in marriage arrangements.

In addition to empirical studies that utilize crossfostering or various early exposure techniques, numerous

mathematical models have been constructed to examine the various aspects of mate-choice imprinting. For example, population genetic models have been used to explore the evolution of different forms of imprinting. In these models, Tramm and Servedio compared the evolution of paternal, maternal, and oblique imprinting and found that paternal imprinting was the most likely to evolve. Their results suggest that the success of a particular imprinting strategy is most influenced by the group of individuals that are imprinted upon (termed the “imprinting set”).

#### **Juvenile Experience: Mate Selectivity**

Mate-choice imprinting involves juvenile individuals imprinting on, or learning, various characteristics of an adult model, whether the model is their mother, father, or another nonparental adult. Subsequently, these learned characteristics are incorporated into the individual’s mate-choice criteria, and mating partners with similar characteristics are preferred. However, experience with conspecific adults may not always lead to a preference for individuals resembling a model. Sometimes, early experience may simply increase choosiness. Such effects of early experience have been documented in various animal taxa. For example, in both field crickets and wolf spiders, research has shown that early experience by females with courtship songs or displays can lead to increased selectivity for mates.

#### **Adult Experience: Mate Selectivity**

Effects of experience on mate choice need not be restricted to young or immature individuals. As adults, encounters with rivals and potential mates can also alter mating behaviors for both males and females. For example, in some spiders, fruit flies, crickets, and newts, na-

ive females are less discriminating in mate choice than older and more experienced females. A female's threshold to accept a male can also change with successive encounters, both pre- and post-mating. Presumably, as females gain experience with mates, they learn to distinguish among them. A significant literature exists on female search strategies (e.g., sequential search, best-of-*n*, and variable threshold), many of which implicitly assume learning.

Not only do adult females alter their mate choice based upon their personal experiences with mature males, but they may also alter their preferences based on personal information regarding their own attractiveness. In humans, for example, attractive females have stronger preferences for high-quality males than less attractive females, and in zebra finches, a female's self-perception has been shown to influence her mate choice. In nature, this self-assessment may or may not be learned, but theoretical models suggest that the perception of one's own attractiveness could develop through previous experiences with the opposite sex, resulting in increased choosiness following successful encounters and decreased choosiness following rejection by potential partners.

Thus far, we have been focusing mostly upon female mating preferences. However, males have also been shown to alter mating behaviors with experience. As males are rejected or accepted by females, they may become more or less sexually aggressive and/or more or less discriminating. Trinidad guppy males, for example, learned to direct courtship at conspecific females after 4 days of contact with conspecific and heterospecific females. In damselflies, males prefer females of a morph with which they have had previous experience. In *Drosophila*, a male's experience with a heterospecific female often leads to reduced future courtship effort toward heterospecific females. In wolf spiders, previous mate effects are known to shape a male's future mating success. Males that had experienced, but not mated with, a female were less likely to mate in the next encounter. However, if the male had mated with the previous female, it was more likely to mate with the next.

## Public Information

### Adult Experience: Mate-Choice Copying

In various taxa (although primarily in fish and birds), females observe and copy the mating decisions of conspecific females. In some cases, mate-choice copying leads to an increased preference for the male traits observed in the mated male. In other cases, females may prefer the actual male that was observed mating with another female. Mate-choice copying has the benefit of decreasing the investment in mate assessment that a female must make. The reliability, consistency, and agree-

ment between sources of information available to a female may determine when a female copies mating decisions and when she will forego mate-choice copying, relying instead on private assessment. In some species, when public and private information conflict, females base decisions on their own assessment, while in other species, females revert to mate-choice copying in such situations. In humans, mate-choice copying has been documented to depend on the quality of the model female observed with a potential mate. Additionally, in humans as well as other taxa, the degree to which females will copy mating decisions of others is influenced by sexual experience. In many cases, virgin females are more likely to copy mate-choice decisions than more sexually experienced females. Mate-choice copying has been documented in vertebrate (e.g., fish, birds, and mammals) and invertebrate (e.g., insects) species.

## Mechanisms of Mate-Choice Learning

Identifying and describing the physiological mechanisms that underlie the relationship between learning and mate choice is a vast area of research. Here, some of the major findings of the field are summarized. The neurophysiology of early mate-choice imprinting in zebra finches has been extensively explored. Immediate-early genes (*c-fos* and *ZENK*) have been used to estimate neuronal activity and to identify activated brain regions with exposure to novel and previously experienced stimuli. Researchers have also investigated neuronal control of the length and timing of the sensitive period for sexual imprinting. In *Drosophila*, the neurosensory pathway that functions in the male and female brain to determine whether to attempt courtship with a potential mate based on previous experience, has been described. In mice, after investigating the volatile chemical signals present in female urine, males acquire more complex and extensive preferences for the odor of sexually receptive females. These male preferences correspond to changes in the piriform cortex of the brain, and knockout studies have demonstrated that the gene *Peg3* disrupts these effects of experience. Thus, in disparate taxonomic groups, significant information is available on the physiological mechanisms underlying mating choice learning, and this remains an active area of research.

## Evolutionary Consequences of Mate-Choice Learning

One of the most intriguing and intellectually stimulating aspects of mate-choice learning is its potential to drive evolutionary change. Not surprisingly then, exploring the evolutionary consequences of mate-choice learning is an extremely active area of research, rich with theory and modeling. The most frequently discussed aspects of

mate-choice learning involve its putative influence on such evolutionary processes as speciation, hybridization, and sexual selection.

### **Speciation and Mate-Choice Learning**

It has frequently been suggested that mate-choice imprinting can facilitate reproductive isolation. Imprinting on one's parental phenotype, for example, leads to positive assortative mating, where similar phenotypes preferentially mate with each other. Any new phenotype, or novel trait, appearing in a population could rapidly lead to reproductive isolation via mate-choice imprinting, even if it is initially present at a low frequency. Empirical work with collared flycatchers (*Ficedula albicollis*) has provided support for such a mechanism, as the artificial introduction of a novel trait (a red stripe on a male's forehead) led to positive assortative mating – females having experienced males with a red stripe were more likely to pair with males possessing red stripes. The initial effects of such mate-choice imprinting could then be followed by disruptive selection. In fact, a recent mathematical model has demonstrated that reinforcement (enhancement of premating isolation) can occur via learned mating preferences. It is important to note, however, that the influence of mate-choice imprinting on evolutionary processes such as speciation depends implicitly upon the imprinting set, or the individuals used as models. For example, imprinting on a nonparental phenotype (oblique imprinting such as mate-choice copying) would likely inhibit population divergence. Nonetheless, the involvement of mate-choice imprinting on speciation and diversification has likely been important for numerous taxonomic groups and has been explicitly suggested to have played a role in the diversification of various birds (e.g., Galapagos finches; various brood parasites) as well as fishes (e.g., Lake Victoria cichlids).

The occurrence of interspecific brood parasitism raises unique questions with respect to the evolutionary implications of mate-choice imprinting. Consequently, a significant amount of research addresses the role of mate-choice imprinting on speciation and diversification in avian brood parasites. Interspecific brood parasites constitute approximately 1% of all bird species and are defined as those species for which adults do not care for their young, but instead deposit their eggs in the nests of other species, where the young are left to be raised by foster parents. Given the common occurrence of mate-choice imprinting in birds, an obvious question arises regarding how imprinting on a foster parent might influence subsequent reproductive success of the parasitic offspring. For example, if parasitic offspring imprint on visual aspects of their foster parent, their subsequent ability to find a conspecific mate could be severely compromised. However, imprinting on the song of the foster parent (which can be learned),

for both males and females, could facilitate conspecific matings. Indeed, in whydahs and indigobirds (interspecific brood parasites in the genus *Vidua*), parasitic male offspring copy the song of their foster fathers. Parasitic female offspring also imprint on their foster father's song. This host imprinting ultimately enables parasitic offspring to find conspecific mates as adults. This process of host imprinting has been proposed as a mechanism promoting diversification in this group, as host shifts could readily lead to reproductive isolation. However, one could also imagine a scenario where mate-choice imprinting on a host could lead to hybridization. For example, if numerous species utilize the same host, the likelihood of parasitic individuals mating with a heterospecific brood parasite increases, and recent work has indicated that continued gene flow does exist between some host races.

### **Hybridization and Mate-Choice Learning**

Although mate-choice imprinting often results in positive assortative mating, typically with conspecifics, the potential exists for misimprinting, or imprinting on the wrong species. Hybridization between species of Darwin's finches, for example, is known to occur and is thought to result from misimprinting. Additionally, crossfostering experiments conducted in the wild have demonstrated that some bird species will imprint on a foster parent of another species, resulting in heterospecific pairings.

Heterospecific matings could result in hybrid offspring and hybrid zones are not uncommon in nature. What role then, if any, does mate-choice imprinting play in hybrid zones? Using an artificial neural network, Brodin and Haas demonstrated that phenotypes of pure species are learned faster and better than those of hybrids, potentially leading to selection against hybrids. Further spatial simulations combined with empirical data on dispersal demonstrate that mate-choice imprinting can maintain a hybrid zone under natural conditions.

### **Sexual Selection and Mate-Choice Learning**

In addition to its role in speciation and hybridization, mate-choice learning might also lead to the evolutionary change of specific traits within a species, especially traits that are sexually selected. For example, mate-choice imprinting can lead to sexual preferences for extreme phenotypes beyond which an individual has experienced, potentially driving trait elaboration. One mechanism by which this is possible is via peak shift – a consequence of discrimination learning of differentially reinforced stimuli (e.g., individuals are trained such that one stimulus is rewarded and the other is punished). Essentially, peak shift can lead to a preference for an ex-

aggerated trait never previously experienced. For example, in an elegant study using zebra finches, ten Cate and colleagues raised males with the parents of artificially painted beaks (orange or red). In subsequent mating trials, they were able to show a shift in male beak color preference, with males directing more courtship to females at the extreme maternal end of the spectrum, despite the fact that this beak color was more extreme than seen in the model parent.

The above-mentioned example addresses the role of parental imprinting on trait evolution. However, oblique imprinting, or imprinting on a nonparental adult, also has intriguing potential regarding the evolution of secondary sexual traits. The cultural transmission of mating preferences, or passing on of mating preferences through nongenetic mechanisms, could lead to evolutionary changes in secondary sexual traits, or cultural inheritance. Cultural transmission refers to the process by which the phenotype of a species can change based upon information acquired during an individual's lifetime. Essentially, the cultural transmission of female preferences (via juvenile experience effects with nonparental adult conspecifics or via mate-choice copying) could drive the cultural inheritance of male secondary sexual traits. The details of such evolutionary change would depend explicitly on the form of imprinting and on the imprinting set.

### **Genotype-by-Environment Interactions and Mate-Choice Learning**

Thus far, we have focused solely on various environmental effects on mate-choice learning, with no discussion of the underlying genetics. Yet, all organisms are influenced by both their genes and their environment. Much recent work has been directed explicitly at understanding the interactions between an individual's genotype and its environment. Genotype-by-environment interactions (GEIs) have become one of the major explanations regarding the maintenance of genetic variation in secondary sexual traits, despite putatively strong sexual selection that should diminish this variation. While most studies of GEIs have focused on male signaling traits, it seems equally likely that female preferences are influenced by GEIs. For example, a female's genotype may impact her likelihood and/or her ability to learn mating preferences. Such GEIs with respect to mate-choice learning would certainly influence the interactions between learned mate choice and the evolution of male secondary sexual traits. Future work exploring the interactions between genotypes and social environments will surely provide a rich source of new knowledge and insights regarding mate-choice learning and its role in evolutionary processes.

**See also:** Alex: A Study in Avian Cognition; Apes: Social Learning; Avian Social Learning; Behavioral Ecology and Sociobiology; Collective Intelligence; Costs of Learning; Cultural Inheritance of Signals; Culture; Decision-Making; Foraging; Fish Social Learning; Flexible Mate Choice; Imitation: Cognitive Implications; Insect Social Learning; Isolating Mechanisms and Speciation; Learning and Conservation; Mammalian Social Learning: Non-Primates; Mate Choice in Males and Females; Memory, Learning, Hormones and Behavior; Monkeys and Prosimians: Social Learning; Psychology of Animals; Sexual Selection and Speciation; Social Cognition and Theory of Mind; Social Information Use; Social Learning: Theory; Vocal Learning.

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