

## S18-5 Sexual signals, learning processes and evolution

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**Abstract** Examples are given of how the widespread learning processes of sexual imprinting, song learning and song preference learning may affect the evolutionary processes of sexual selection and speciation in birds. They show that sexual imprinting may occur together with perceptual biases, giving rise to preferences for mates with exaggerated traits. Sexual imprinting may also give rise to exaggeration of sexual dimorphism through “peak shift”, a by-product of discrimination learning. Imprinting and song (preference) learning seem responsible for enabling or driving the rapid speciation of some avian brood parasites. The examples highlight the point that learning processes can have a profound impact on evolutionary processes and deserve prominent attention in evolutionary theory.

**Key words** Imprinting, Mate choice, Evolution, Speciation, Sexual selection, Song learning

### 1 Introduction

Birds are frequently used as model species to examine such evolutionary processes as sexual selection or speciation. A central element in theories about these processes concerns variation in the signals involved in mate choice (sexual signals) and in the preferences for these signals. In birds, sexual signals are predominantly visual (plumage color or pattern) or acoustic (voice). But how do birds “know” to which signals they should respond in order to get the right mates? Many models of evolutionary processes assume that genetic disposition underlies trait recognition and preference. Yet learning processes too are very important in the development of such preferences in birds, and even in the development of some signals used in mate choice. Although increasing attention is now being paid to understanding how learning may affect evolutionary processes, relatively few studies as yet address this issue. In this paper I review a number of such studies, concentrating on the role of sexual imprinting and song learning.

### 2 Is learning important?

It has long been known that many bird species use parents as models for future mate preference: they learn from them and later prefer similar-looking mates. Such “sexual imprinting” was initially thought to be limited to special cases, notably rapidly evolving species (Immelmann, 1975). However, ten Cate and Vos (1999) have demonstrated that the phenomenon is widespread, revealing its presence in over hundred species, including members of most bird orders. Acquiring mate preference through learning thus seems the rule, not the exception, in birds.

With respect to vocal signals (songs), a distinction needs to be made between learning involved in the production of signals and learning that leads to specific preferences.

Sound production learning has been demonstrated for songbirds (oscines), hummingbirds and parrots. It may be present in some other groups, but it is also clear that several taxa can only produce the voice of their own species after cross-fostering or rearing in isolation. Less clear is the situation with respect to vocal recognition learning. Females of several species, particularly in songbirds, are known to prefer songs heard early in life. Learning may not be limited to songbirds, but for most other groups it is largely unknown whether females have to be exposed to conspecific calls if they are to respond to them later on. It is clear that both imprinting and song learning are important in birds, raising the question of their impact on evolutionary processes. Three examples of this impact follow.

### 3 Imprinting and sexual selection

The traditional view of sexual imprinting is one of a mechanism that enables species recognition. Both theoretical and empirical studies have concentrated on the impact of imprinting on choosing conspecifics over heterospecific mates, or choosing conspecifics of one particular color morph over another. It has even been said that imprinting results in mate preference for “those objects bearing the closest similarity to the original stimulus” (Immelmann, 1975). No wonder then that imprinting was not seen as a mechanism important in sexual selection, which implies the presence of biased preferences. This view has now changed, largely as a result of imprinting studies on Japanese quail. When raised with siblings, male and female quail both preferred to mate with birds of the same wild-type morph as their siblings; but among these individuals they preferred mates slightly different from siblings: first cousins were preferred, both over siblings and over more distantly related birds (Bateson, 1982). Other experiments have shown that males and females prefer mates with traits missing from

their parents. Thus in the zebra finch — a model species for studying imprinting — both males and females preferred mates with artificial additions such as colored leg bands or a white feather in the head (Burley and Symanski, 1998).

So how do imprinting processes and perceptual preferences interact? This has been examined systematically in further experiments on the Japanese quail. The experiments were designed to address the question: do quail that are free to choose novel birds which differ from imprints in a specific, experimentally controlled way have a bias in choice? In the experiment, young quail were exposed only to white adults during parenting. For one group, the white adults had six black dots dyed on the breast, for another group three, and for the third none. When mature, the young quail were given choice tests. When given the choice between a bird similar to the imprinting stimulus and a wild type, the imprinted bird was preferred. However, among three white types, those with the highest number of dots were preferred significantly over the lowest, irrespective of the number of breast dots in original stimulus imprinting adults (ten Cate and Bateson, 1989). This experiment suggests that imprinting may set a standard for the mate preference, which is combined with an additional perceptual bias, leading to asymmetric preference for novel mates.

Such a mechanism might drive sexual selection (ten Cate and Bateson, 1988), leading individuals to mate with those birds showing parental traits that had diverged slightly in an exaggerated way. Offspring of such a pair would not only be likely to inherit the exaggerated trait (if based on genetic variation), but would also use it as a standard for their own preference later, thus linking trait and preference. Subsequent studies on Javanese mannikins (Witte et al., 2000) and zebra finches (Witte and Sawka, 2003) have confirmed that imprinting on novel or artificial traits can occur, although the effects may differ between sexes and also in relation to the trait itself. Recent theoretical modeling, moreover, suggests that sexual imprinting in combination with an asymmetric bias in preference alters the dynamics of the sexual selection process and may speed up the evolution of conspicuous traits (Laland, 1994; Aoki et al., 2001).

It can be concluded that sexual imprinting is not only present in species that select sexually, but may even contribute to the dynamics of the process. More experimental work is required, in particular, to elucidate the proximate and ultimate factors that give rise to variation in outcome between sexes and species.

#### 4 Sexual imprinting and sexual dimorphism

In many species, sexual selection is supposed to be the driving force behind sexual dimorphism in appearance, e.g. in plumage pattern or coloration. If imprinting can generate plumage evolution under sexual selection, how is it implicated in the origin and maintenance of sexual dimorphism? Sexual dimorphism can arise if males and fe-

males of a species have different sexual preferences. This may be brought about in different ways. For example, males and females may differ in their balancing of sexual imprinting with respect to other mechanisms that guide visual preferences, such as perceptual biases (see above). A proper interpretation of studies purporting to show a sex difference in the outcome of the mating process in cross-fostered individuals is complicated, however, due to behavioral interactions between males and females that may obscure initial preferences for certain plumage types (ten Cate and Vos, 1999).

It is clear, nevertheless, that perceptual biases which interact with learned preferences may differ between the sexes. Also, although learning may influence both sexes, the sexes may differ in what they learn and from whom (ten Cate and Vos, 1999). For example, in the sexually dimorphic zebra finch, males develop a preference for females of similar appearance to their mother (Vos et al., 1993). And for female zebra finches, recent evidence indicates that they are more likely to imprint on their father than on their mother (Witte and Sawka, 2003). Such differential learning may facilitate the maintenance, even exaggeration, of sexual dimorphism in appearance. It shows that sexual imprinting as a mechanism is compatible with the existence of such dimorphism.

There is one further particularly interesting question: does the imprinting process itself induce its own bias towards more extreme traits, independently of perceptual biases. Several authors (e.g., Weary et al., 1993; ten Cate and Vos, 1999) suggested that sexual imprinting might lead to the enhancement of sexual dimorphism through a phenomenon known as “peak shift”. Peak shift occurs in circumstances of discrimination between two stimuli that differ slightly on one dimension. Thus an animal can learn that response to a light of one wavelength results in reward and to another in punishment. When subsequently tested with signals spanning a wider range of wave lengths, the peak response may shift to signals that exaggerate the difference between the training stimuli. A starting point for examining whether sexual imprinting may induce peak shift was the finding that male zebra finches raised by foster parents of a wild type male and a white female or vice versa, not only preferred females of their mother’s morph, but actively avoided females of the father’s morph (Vos et al., 1993). A subsequent experiment showed that zebra finch males raised by white parents differing only in beak color (red in fathers, orange in mothers) preferred females with orange beaks over those with red (Vos, 1995; ten Cate and Vos, 1999). Taken together, these experiments provide evidence for discriminatory learning during imprinting, at least among males.

The experiments also provide a model for testing whether such discriminatory learning results in peak shift: what does the preference look like when males are tested with females varying in beak color along the red/orange scale? In a preliminary experiment, males were exposed to white parents with bills painted red or orange with nail polish.

This treatment enabled experimental control for color variation, and also made it possible to generate one group in which the fathers had orange beaks and the mothers red, and a second group in which the beak colors were reversed. Later on, males were tested with females differing in beak color. Only in the father-orange, mother-red group was there a shift towards a more extreme preference (ten Cate and Vos, 1999). The experiment, however, was not conclusive, and a more extensive and rigid test is in progress. Preliminary data seem to confirm the presence of a peak shift. If present, this mechanism should drive modest sexual dimorphism towards more extreme differences as an ‘artifact’ of the imprinting process itself.

## 5 Sexual imprinting as a mechanism inducing speciation

Various researchers have concluded that imprinting does generate assortative mating and by doing so can contribute to speciation (e.g., Laland, 1994; Grant and Grant, 1997; Irwin and Price, 1999; ten Cate and Vos, 1999). Here follows an unusual and special example of a speciation process in which imprinting has an active role, in this case combined with song learning. It concerns the speciation process in a group of avian brood parasites, the viduid finches (indigobirds and whydahs), which parasitize estrildid finches. Most viduid finches are specialized parasites, laying their eggs in the nests of specific host species and developing clear adaptations to that host, e.g., young resemble nestlings of the host species in mouth markings and plumage (e.g., Nicolai, 1964). Male viduids, moreover, sing species-specific songs that strongly resemble those of the host species (Nicolai, 1964; Payne, 1973). Female viduids are attracted to that particular song type over others (Payne, 1973; Payne et al., 2000). The song of the host species stimulates ovarian development in parasitic females, and attracts them to its nests. The morphological similarities between parasite and host offspring, and the host-oriented behavior of the parasitic viduids, suggest a long history of co-evolution between host species and their specific parasites. Indeed, Nicolai (1964) suggested that viduid species had evolved jointly with their hosts.

Yet recent DNA-studies make this scenario unlikely. They show not only that the most likely phylogenetic branching patterns of hosts and parasites do not match, but also suggest that speciation in the parasites has occurred substantially more recently than in the hosts. These observations support an alternative model for evolution, that of ‘colonization, in which a parasitic lineage switches from one host species to another, leading to subsequent adaptation to the new host (Payne et al., 1998, 2000). But although one can imagine a female parasite laying her egg in the nest of a new host species, this still seems to be a long way from founding a new branch on the species tree.

The key to understanding how a parasitic species can colonize a new host with apparent ease and become reproductively isolated from its ancestor at the same time

lies in the mechanisms that guide host selection, mate preferences and mate attraction signals. Viduid finches are songbirds and, as in other songbirds, learning is important in developing songs as well as song preferences. Payne et al. (1998, 2000) demonstrated that when village indigobirds (*Vidua chalybeata*), which normally parasitize firefinches (*Lagnostica senegala*), were cross-fostered to Bengalese finches (*Lonchura striata*), they developed a distinctly different song. Instead of singing the usual repertoire of firefinch-like songs, they sang Bengalese finch-like songs. Moreover, cross-fostered females, which normally prefer village indigobirds singing firefinch songs, now preferred mates singing Bengalese finch-like songs. When these females were later introduced to aviaries of several potential host species, including firefinches and Bengalese finches, they preferentially laid their eggs in the nests of Bengalese finches, i.e. nests belonging to the species which raised them.

Thus, a parasitic female that lays her eggs in the nest of a novel host will produce offspring that differ substantially from their biological parents in behavior, producing parasitic individuals that have taken important steps towards colonizing the new host. Coincidentally, the same changes produce a reproductive break with conspecifics raised by the traditional host. If successful with the new host, the traditional Darwinian mechanisms of genetic mutation and selection might later lead to morphological adaptations (e.g., in nestling mimicry of mouth markings), eventually budding off a new parasitic species. So, the rapid speciation in viduid finches seems to be the outcome of an evolutionary process in which behavioral changes that result from early learning are the catalyst.

To conclude, the presence of learning processes in signal making and signal reception in mate choice affects evolutionary processes in several, and sometimes surprising, ways. It is clear that much is still to be discovered.

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