

Short Review

Sexual imprinting, learning and speciation

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Learned mate preferences may play an important role in speciation. Sexual imprinting is a process whereby mate preferences are affected by learning at a very young age, usually using a parent as the model. We suggest that while the origins of learning appear to lie in the advantages of individual recognition, sexual imprinting results from selection for recognition of conspecifics. This is because efficient early learning about one's own species is favoured in the presence of heterospecifics. If different species are hybridizing, both sexual imprinting and learning to avoid heterospecifics during adulthood promote assortative mating and hence speciation. As a

result of sexual imprinting, speciation may also be completed in allopatry when divergence between populations is sufficient to prevent interbreeding when the populations reunite, even in the absence of genetic evolution of mate preference. The role of behaviour and learning in completing the speciation process is relatively overlooked. In particular the evolution of sexual imprinting as a result of selection against hybridization warrants more study.

Keywords: birds, hybridization, imprinting, reinforcement, reproductive character displacement, song recognition, speciation.

Sexual imprinting has been defined as the means by which a young bird learns species-specific characteristics that enables it to find a conspecific mate when adult (Bateson, 1966; Clayton, 1993). These characteristics are usually learned from the parents. Mating preferences acquired as a result of sexual imprinting are often difficult to modify by subsequent experience (Lorenz, 1937; Bateson, 1966). Sexual imprinting is widespread, having been demonstrated in over half the orders of birds (Ten Cate *et al.*, 1993), and similar processes are observed in other taxa (Hinde, 1961; Immelmann, 1972; Kendrick *et al.*, 1998). Immelmann (1972; p. 166) summarizes the prevailing view on the role of imprinting: 'the most important function of sexual imprinting is to enable the birds to recognize members of their own species and thus to ensure that, under natural conditions, sexual behavior and pair formation displays are restricted to conspecific mates.' The emphasis on species recognition suggests a key role for imprinting in the speciation process itself (Immelmann, 1975; Laland, 1994; Grant & Grant, 1997a,b, 1998).

We review the role of imprinting and other forms of recognition learning in speciation. This is a neglected area, and some of the more relevant contributions were made more than 100 years ago. Howard (1993) refers to a series of papers by J. Gulick in the 1890s who discussed how behavioural differences leading to the partial isolation of populations create conditions ripe for further population divergence. Spalding (1873) cogently outlined how learned recognition behaviours could evolve into innate recognition mechanisms as a consequence of selection, a process now known as assimilation (Waddington, 1953, 1959; Fear & Price, 1998). While the importance of behaviour in speciation has been addressed in many more recent publications, the emphasis has been on how

behavioural changes initiate the speciation process. First, novel behaviours such as the exploration of a new environment can place new selection pressures on a population (Mayr, 1970; pp. 363–364; Wcislo, 1989). Secondly, behavioural traits involved in courtship and mating diverge between populations as a result of drift and selection (Martens, 1996; Price, 1998). These studies are more concerned with how traits suitable to be used in species recognition diverge between populations, and less with how the recognition mechanisms themselves arise. By considering the role of learning in recognition we are examining the last stage of speciation, whereby complete premating isolation becomes established between divergent populations.

One reason to consider behavioural mechanisms in speciation is that they potentially affect the rate at which species can form. Felsenstein (1981) noted that there were few ecological constraints preventing population divergence and asked why speciation was not more common than it appears to be. He investigated possible genetic reasons that might limit speciation rates. He started with a model where some postmating isolation between two populations is present, and asked how easily premating isolation could arise and spread. There are two conditions in which premating isolation might readily spread. These are (i) if genes promoting premating isolation are tightly linked with, or identical to, those promoting postmating isolation, and (ii) if the same allele in each population promotes assortative mating on the basis of those traits that separate the two populations. Both of these conditions may occur in nature. For example, experiments of Rice & Salt (1990) meet condition (i) where the genes promoting premating isolation (habitat choice) are the same as those causing postmating isolation. The evolution of sexual imprinting meets condition (ii) because an allele that causes stronger sexual imprinting is selected in both populations during speciation. This process results in the creation of two

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species where the mechanism of imprinting does not constitute a genetic difference between the species (Seiger, 1967).

We focus on the role of sexual imprinting and other learning in causing assortative mating and thus promoting speciation. However, behavioural mechanisms of mate choice also place a limit on the rate of speciation. Hybridization can result from adaptive mate choice of heterospecifics when there are few conspecifics available (Grant & Grant, 1997a; Nuechterlein & Buitron, 1998) or occasional misimprinting on the wrong species (Grant & Grant, 1997a). Even if there are neither genetic nor ecological constraints on rates of speciation, behavioural mechanisms of mate choice can slow the rate of species formation.

We concentrate on speciation in birds, the group in which sexual imprinting has been most completely studied. First, we consider the role of learning in species recognition and mate choice. We show that although sexual imprinting is generally important, choice of mate can be modified somewhat as a result of experiences with other species and individuals in later life. Next, we consider two basic ways of generating pre-mating isolation between populations. These are (i) complete population divergence in allopatry without any sympatric interaction and (ii) speciation by reinforcement, whereby species recognition is strengthened as a result of selection against hybrids [Dobzhansky, 1940; Howard, 1993; the model of Felsenstein (1981) is an example]. Finally, we ask how recognition mechanisms may facilitate or hinder speciation by these processes.

Learning

Sexual imprinting establishes a 'sort of consciousness of the species in the young bird' (Lorenz, 1937) which is then used in mate choice. It can be quite inflexible. Lorenz relates one story about a male bittern which was raised by a zoo-keeper. Although the bittern was maintained with a female of its own species and eventually paired with it, the misimprinted male would drive the female away whenever the zoo-keeper approached, and try to get the keeper to come into the nest to incubate the eggs. Subsequent controlled experiments have confirmed the power of sexual imprinting. For example, Oetting *et al.* (1995) allowed young male zebra finches *Taenopygia guttata* to be reared by Bengalese finches *Lonchura striata* until they were 40 days old and then kept them in isolation for another 60 days. Males subsequently briefly exposed to a female Bengalese finch always strongly courted Bengalese finches in choice tests; males briefly exposed to a female zebra finch still showed stronger preferences for female Bengalese finches than female zebra finches. Several cross-fostering experiments in the wild have resulted in hybrid pairings attributed to sexual imprinting on the foster parent (Harris, 1970; Fabricius, 1991).

Sexual imprinting arises as a consequence of learning about individuals and can create mate preferences within species. Male zebra finches prefer females with similar characteristics to their mother (Vos, 1995). Assortative mating in snow geese (Cooke & McNally, 1976) and mate choice in pigeons (Warriner *et al.*, 1963) and mallard ducks (Lorenz, 1937; Kruijt *et al.*, 1982) are affected by colour of the rearing strain.

The effect of this sort of early experience extends across species in nature. Grant & Grant (1997a) show that hybrid pairings in Darwin's finches most commonly occur when parents of the hybridizing bird have similar morphology and/or songs to the heterospecific. Sexual imprinting thus appears to be a result of learning about parents, and generalizing out from those parents to other similar individuals (Fig. 1a,b).

The earliest manifestation of learning in many bird species is seen in filial imprinting, defined as the 'learning process accompanying the following response of nidifugous birds' (Hinde, 1962; Bateson, 1966). For example, chicks readily become imprinted on a red box, and will follow it to the exclusion of other objects. Filial imprinting is separable from sexual imprinting, but the processes are similar in many ways (Hinde, 1962; Bateson, 1966; Immelmann, 1972). In filial imprinting, once the young bird has formed an attachment to a particular object it avoids novel objects (Bolhuis, 1991; p. 310). There are conflicting pressures on the young bird to readily recognize and follow its parent but also to recognize and avoid other adults, as well as heterospecifics that are potential predators (Hinde, 1961). Such conflicting pressures in filial imprinting resemble those involved in sexual imprinting and mate selection, when it is advantageous to distinguish conspecifics from heterospecifics.

Filial imprinting is thought to be widespread because of the importance of individual recognition, and in particular recog-

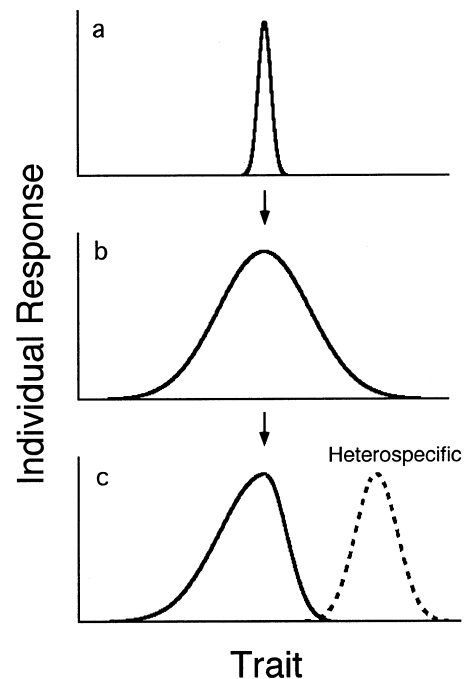


Fig. 1 Model of the development of a female's mate preference curve throughout her life. (a) Distribution of signals which a chick associates with an individual parent. (b) The young bird generalizes its response curve outward from the parent's traits. (c) As a result of experience with a heterospecific which has large trait values, the female preference function contracts on the right side.

dition of the parent. For most species the importance of recognizing individuals does not stop with the parent. Hinde (1962) stressed the role of contingency in the development of preferences, with an animal building on its past experiences. Individual recognition is established in flocks, territorial songbirds recognize neighbours, and individuals recognize their mates (e.g. Schimmel & Wasserman, 1991; Temeles, 1994). Therefore, selection favouring learning of individual characteristics is present throughout life, and mate choice is one manifestation of the general advantage of the ability to identify conspecifics in a variety of social situations.

Discrimination of heterospecifics may also result from learning. We reviewed 10 studies of song recognition between congeneric species of birds in which responses in allopatry and sympatry were compared (Table 1). These are mostly aggressive responses by males to male songs. In none of the cases does the song or call vary significantly between sympatry and allopatry but in nine of the 10 cases there are large differences in response between sympatry and allopatry. In five cases the response was greater in sympatry than allopatry, and this generally reflects interspecific territoriality. In four cases there was the opposite pattern, with the response greater in allopatry than sympatry. While there are two patterns here, all of these cases of different responses in allopatry and sympatry are likely to represent learned reactions to the presence of another species. In several of the cases in Table 1 the sympatric and allopatric areas were often only a few hundred metres apart, making a genetic explanation unlikely.

Learning is thought to be advantageous either because it saves time and energy spent interacting with individuals which do not pose a threat (in the case of decreased response in sympatry), or because it enables a threat to be more readily recognized (in the case of increased response in sympatry). For example, Lynch & Baker (1990) argue that common chaffinches and blue chaffinches have learned to not respond to heterospecific songs in sympatry because the two species use different ecological resources and do not hybridize. In an example of the opposite pattern, Emlen *et al.* (1975) reported that indigo and lazuli buntings respond aggressively to heterospecific song in sympatry but not in allopatry. They attributed this to a learned response to an ecological competitor. These two species hybridize, so heterospecific males are also competitors for mates.

How do birds learn to recognize or discriminate against heterospecifics? We suggest that this behaviour is a continuation of a learning process that develops throughout the life of the bird. We now consider the mechanisms of this process, which begin with filial imprinting. A chick learns an assemblage of traits (e.g. shape, colour, call) when imprinting on a parent, and more readily learns these traits when they are presented at the same time rather than singly (Bolhuis & van Kampen, 1992). Learning continues through subsequent encounters with the parent. As noted by Hinde (1961) a parent appears in many shapes and sizes and against many backgrounds, and this must result in a distribution of perceived traits that result in recognition (Fig. 1a). In laboratory experiments using artificial objects, presentations close

together in time (Honey *et al.*, 1994) or similar in appearance (Bolhuis, 1991; pp. 316–318) are more likely to be classified by a chick as the same object. One consequence can be modifications of filial imprinting to follow different, but similar-looking, individuals. Kent (1987) showed that chicks exposed to live hens for 3 days preferred them over unfamiliar hens in choice tests, but that the preference could be lost after four hours separation from the familiar hen and reversed by further exposure to another hen. These sorts of updates and use of multiple cues may be important in generalizing from filial imprinting on a single individual to conspecifics in social situations later in life (Fig. 1a,b).

In both filial and sexual imprinting, a young bird makes associations between multiple traits, such as colour and call, that distinguish individuals or species. These associations, which reflect true correlations between traits of conspecifics, make it possible to use a single trait in recognition. For example, in many species the chick recognizes the parent's call and will respond to it but not to the call of other conspecifics even in the absence of any visual presentation (Halpin, 1991; pp. 235–240; Aubin & Jouventin, 1998). This is also likely to apply in the case of recognition of heterospecifics by adults. For example, response to an unusual but acceptable song could lead to interactions with an individual of unacceptable plumage, which then could result in learned avoidance of the unusual song in the future (e.g. Fig. 1c). Gill & Murray (1972) argued that the lower response of blue-winged warblers to the song of golden-winged warblers in sympatry than in allopatry (Table 1) results from 'behavioural experience of the birds' and 'learning that a particular song represents a particular plumage type.' Gil (1997) attributes the higher aggression between short-toed and common treecreepers in sympatry to a bird's ability 'to recognize and respond to the song of those heterospecific birds it encounters foraging in its niche.' Learned associations between different forms of signals (call, plumage, movement, etc.) allow an individual to use one of them to recognize individuals that vary in the others.

To summarize this section, we suggest that learned mate recognition results from selection for both individual recognition and species recognition. The benefits of recognizing other individuals are present throughout life, ensuring that the ability to learn traits of others is always in place. This learning process (Fig. 1) can be used for species recognition. Sexual imprinting occurs early in life because parents are reliable models of species-specific characteristics. Mate preferences remain flexible because (i) suitable mates differ from the parents (ii) different individuals provide different benefits, and (iii) heterospecifics should be avoided when hybridization is costly (Grant & Grant, 1997a, 1998). We now consider how sexual imprinting and learning are involved in speciation.

Two modes of speciation

After reviewing the experimental literature Rice & Hostert (1993) suggested two main modes by which speciation can be completed through the evolution of prezygotic isolation. The

Table 1 Cases in which song recognition between two species has been compared between allopatry and sympatry. For each species, the percentage of individuals responding to the other species' song in allopatry and in sympatry is shown, along with sample sizes in parentheses. We also show whether the two species are interspecifically territorial in sympatry and whether they hybridize

Species pairs	Allopatry	Sympatry	Interspecifically territorial?	Hybridize?	References
blue-winged warbler (<i>Vermivora pinus</i>)	78% (9)	22% (18)	No, but occasional interspecific aggression	Yes	Gill & Murray 1972
golden-winged warbler (<i>V. chrysoptera</i>)	14% (7)	14% (14)			
western grebe (<i>Aechmophorus occidentalis</i>)	48% (40)	3% (33)	Interspecific male displays	Very rarely	Nuechterlein 1981;
Clark's grebe (<i>A. clarkii</i>)	—	0% (26)			Nuechterlein & Buitron 1998
black-throated gray warbler (<i>Dendroica nigrescens</i>)	100% (4)	0% (7)	No	No	Morrison 1982
hermit warbler (<i>D. occidentalis</i>)	100% (7)	0% (5)			
common chaffinch (<i>Fringilla coelebs</i>)	88% (8)	9% (11)	No	No	Lynch & Baker 1990
blue chaffinch (<i>F. teydea</i>)	42% (12)	0% (9)			
indigo bunting (<i>Passerina cyanea</i>)	0% (7)	100% (10) ¹	Yes	Yes	Emlen <i>et al.</i> 1975
lazuli bunting (<i>P. amoena</i>)	0% (8)	100% (10) ¹			
reed warbler (<i>Acrocephalus scirpaceus</i>)	0% (10)	0% (10)	Sometimes	No	Catchpole 1977, 1978
sedge warbler (<i>A. schoenobaenus</i>)	N/A	40% (10)			
reed warbler (<i>Acrocephalus scirpaceus</i>)	0% (10)	40% (10)	Yes	No	Catchpole 1978
marsh warbler (<i>A. palustris</i>)	—	No reaction			
reed warbler (<i>Acrocephalus scirpaceus</i>)	0% (10)	60% (10)	Yes	No	Catchpole & Leisler 1986
great reed warbler (<i>A. arundinaceus</i>)	—	—			
alder flycatcher (<i>Empidonax alnorum</i>)	14% (7)	100% (6)	Yes	No	Prescott 1987
willow flycatcher (<i>E. traillii</i>)	29% (7)	100% (8)			
short-toed treecreeper (<i>Certhia brachydactyla</i>)	Greater in sympatry	—	No, but some interspecific aggression	No	Gil 1997
common treecreeper (<i>C. familiaris</i>)	—	—			

¹ For the sympatric playbacks, a total of 10 birds were tested. These included indigo and lazuli buntings as well as hybrids. Separate numbers for each group were not reported, but all responded strongly to both indigo and lazuli song.

first is when premating isolation arises as a correlated response to population divergence in various traits, driven by natural and sexual selection (Fig. 2, left). The second is when premating isolation between populations is generated by selection against hybrids (Fig. 2, right). This mechanism of speciation has been controversial (Howard, 1993), because both experiments (Rice & Hostert, 1993) and theory (Liou & Price, 1994) show that hybrid fitness must be very low or zero for premating isolation to evolve. Even when there is no gene flow between populations because postmating isolation is complete, we consider the evolution of premating isolation to be part of the speciation process (cf. Butlin, 1987; Rice & Hostert, 1993; Liou & Price, 1994). In birds in particular many hybrid pairings produce fertile offspring (Grant & Grant, 1997b) but these hybrids may sometimes suffer reduced viability and reproductive success for various ecological and social causes. If postmating isolation arises for such environmentally contingent reasons, it can easily break down (Grant & Grant, 1996). The only factor maintaining the species as separate entities would then be any premating isolation that had evolved. Thus we follow Howard (1993) in defining the term reinforcement as the evolution of pre-zygotic isolating barriers in response to selection against hybridization, whatever the level of hybrid fitness (as implied also by Dobzhansky, 1940).

Howard (1993) searched for evidence of reinforcement by reviewing studies that compared closely related pairs of species

in sympatry and allopatry. Divergence in courtship signals or increased discrimination of those signals in sympatry is predicted under a reinforcement hypothesis: the *pattern* of increased divergence in sympatry is termed reproductive character displacement (Howard, 1993; cf. Butlin, 1987; Liou & Price, 1994). In 33 of 48 (69%) possible examples Howard (1993) detected reproductive character displacement. Because many of the species still form hybrid pairs the pattern is support for a process of reinforcement. Eighteen of the 48 possible cases concern displacement in discrimination of signals rather than in the signals themselves (they include one case which is in Table 1). Fourteen of these 18 (78%) show reproductive character displacement. Patterns of reproductive character displacement in discrimination appear to occur at about the same frequency as those in courtship traits (chi-square test, $\chi^2_1 = 0.5$, $P > 0.4$). Gerhardt (1994), Noor (1995) and Rundle & Schluter (1998) present additional examples in which reinforcement appears to be a result of increased discrimination in sympatry rather than any change in male courtship traits. However, not all cases of increased discrimination in sympatry are attributable to learned mate recognition. For example, Gerhardt (1994) tested (sympatric) female tree frogs drawn from some ponds where the heterospecific male was absent, and Noor (1995) maintained his naturally sympatric *Drosophila pseudoobscura* stocks in the lab for several generations before testing.

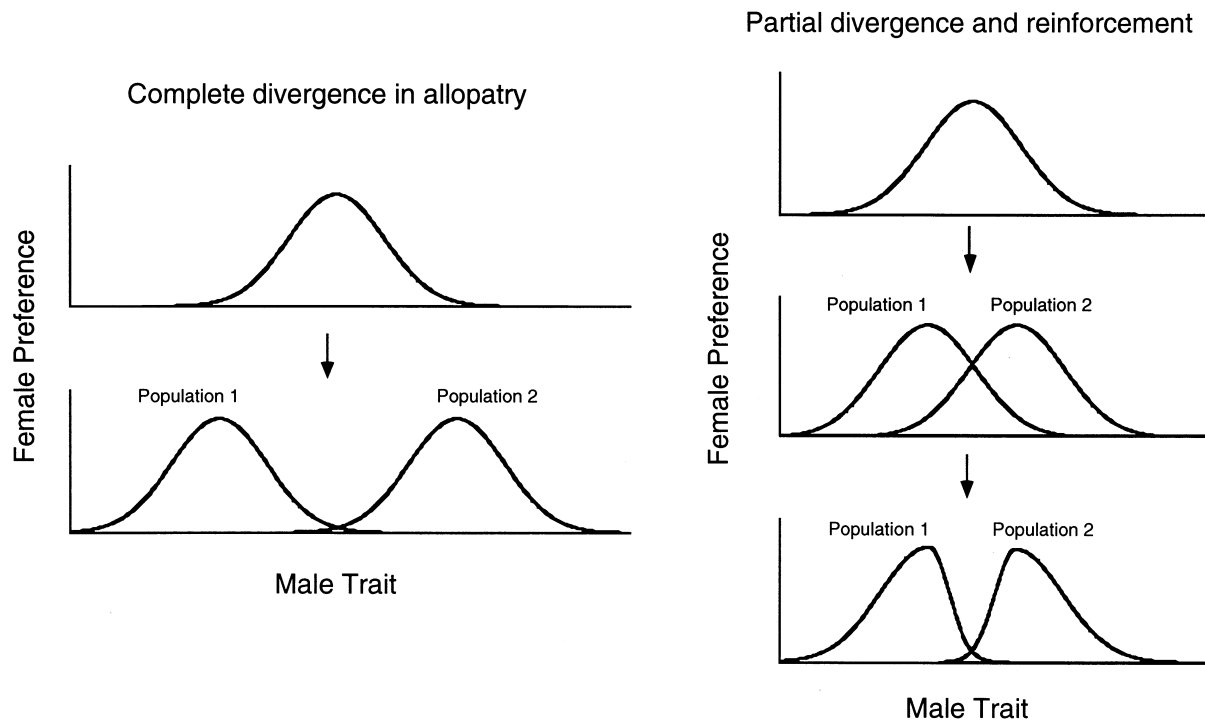


Fig. 2 Two basic ways that learning can promote speciation. Left: male traits diverge after a single population is split into two, and sexual imprinting causes female mate preferences to diverge as well, so that complete assortative mating is present when the two populations come into contact. Right: male traits diverge after a single population is split into two, but isolation is not complete when sympatry is re-established. Increased discrimination arises in sympatry as a result of learning in adulthood. This increased discrimination may subsequently be assimilated into early learning (sexual imprinting).

Learning and speciation

Complete divergence in allopatry

It is easy to see how sexual imprinting, by promoting assortative mating, could result in reproductive isolation if allopatric divergence has been sufficient so that the preference curves are not overlapping (Fig. 2, left e.g. Laland, 1994). This has been most elegantly demonstrated by Clayton (1990), who studied two subspecies of zebra finch. The subspecies are currently separated by 600 km of ocean and are unlikely to have ever been in sympatry, but mate assortatively by subspecies when placed together in large cages (in no-choice situations they hybridize and produce viable, fertile offspring). Cross-fostering experiments were used to show that assortative mating is due to imprinting. When Clayton placed cross-fostered young together in an aviary they all paired with mates resembling their foster parents. Much of this effect is due to females imprinting on attributes of their foster-father, rather than any change in song or plumage of the cross-fostered males.

Reinforcement

In general, the presence of heterospecifics in the environment seems to provide the stimulus for increased mating discrimination (Ratcliffe & Grant, 1983; Grant, 1986, chapter 9; Noor, 1997). When the increased discrimination can be attributed to interactions between hybridizing species it may promote reinforcement (Fig. 2, right). The nine examples in Table 1 in which responses in sympatry and allopatry differ are not all clear examples of reinforcement for three reasons. First, some pairs may never have hybridized, although hybrids have been recorded in three of the interacting pairs. Secondly, the increased discrimination itself may not result in reduction of hybridization. However, Gill & Murray (1972; p. 292) suggest that in the case of the blue-winged and golden-winged warblers learning to avoid heterospecifics does retard the rate of introgression between the two species. Thirdly, the male–male interactions summarized in Table 1 lead to both increased and decreased aggressive response in sympatry. However, even if males respond to each other, females are often more discriminating and therefore avoid heterospecifics during pair formation. For example, male indigo and lazuli buntings respond aggressively to each other in sympatry (Table 1), but hybrid pairs are rare (Emlen *et al.* 1975).

The probability of speciation by reinforcement is reduced by a high level of hybridization, which can cause massive introgression between incipient species or extinction of the rarer species (Liou & Price, 1994). Therefore, whenever learning reduces hybridization it should facilitate reinforcement. We suggest that selection for increased pre-mating isolation between incipient species causes sexual imprinting on the parent to become less modifiable by later experience, or recognition to become directly inherited from parent to offspring (Spalding, 1873). A possible consequence of the reinforcement process is that learning to avoid heterospecifics during adulthood is replaced by an inherent avoidance mechanism, and the avoidance behaviour itself is thereby assimilated into the genotype. The basic genetic and selective

mechanisms underlying this kind of assimilation are discussed in further detail by Waddington (1959) and Fear & Price (1998, fig. 6). Strengthening of sexual imprinting, while being a likely result of reinforcement during one speciation event (Grant 1986, chapter 9), may also increase the likelihood of future speciation events. This is because stronger sexual imprinting reduces the amount of divergence in male traits necessary to prevent interbreeding between populations. Hence, successive speciation events in which reinforcement plays a role may have a cumulative effect on the rate of speciation.

Conclusions

The process we outline in the previous paragraph, while plausible, has never been studied. Nevertheless a role for learning in reinforcement may be widespread. In laboratory experiments Kim *et al.* (1996) show the importance of social interactions with other closely related species for the refinement of mating preferences in *Drosophila paulistorum*. The innate reinforcement of pre-mating isolation documented in *D. pseudoobscura* (Noor, 1995) may have originally been a learned mechanism that has become assimilated.

Our main conclusion is that learning likely plays a major role in speciation in birds, because sexual imprinting is such an important means of identifying conspecifics. Sexual imprinting is a trait whose degree of expression has likely been modified by selection for efficient species recognition, as implied in the writings of many students of behaviour (e.g. Lorenz, 1937; Bateson, 1966; Immelman, 1972; Clayton, 1993). When speciation is completed by reinforcement, learning about heterospecifics later in life may facilitate the process, but this needs study. What is clear is that learning is of widespread importance in species recognition. In birds at least, this apparently arises out of the advantages of recognizing and responding to individuals through a learning-based system throughout life. Individual recognition mechanisms can be easily co-opted into species recognition mechanisms.

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References

- AUBIN, T. AND JOUVENTIN, P. 1998. Cocktail-party effect in king penguin colonies. *Proc. R. Soc. B*, **265**, 1665–1673.
- BATESON, P. P. G. 1966. The characteristics and context of imprinting. *Biol. Rev.*, **41**, 177–220.
- BOLHUIS, J. J. 1991. Mechanisms of avian imprinting: a review. *Biol. Rev.*, **66**, 303–345.
- BOLHUIS, J. J. AND VAN KAMPEN, H. S. 1992. An evaluation of auditory learning in filial imprinting. *Behaviour*, **122**, 195–230.
- BUTLIN, R. K. 1987. Species, speciation and reinforcement. *Am. Nat.*, **130**, 461–464.
- CATCHPOLE, C. K. 1977. Aggressive responses of male sedge warblers (*Acrocephalus schoenobaenus*) to playback of species song and

- sympatric species song, before and after pairing. *Anim. Behav.*, **25**, 489–496.
- CATCHPOLE, C. K. 1978. Interspecific territorialism and competition in *Acrocephalus* warblers as revealed by playback experiments in areas of sympatry and allopatry. *Anim. Behav.*, **26**, 1072–1080.
- CATCHPOLE, C. AND LEISLER, B. 1986. Interspecific territorialism in reed warblers: a local effect revealed by playback experiments. *Anim. Behav.*, **34**, 299–300.
- CLAYTON, N. S. 1990. Assortative mating in zebra finch subspecies, *Taeniopygia guttata guttata* and *T. G. Castanotis*. *Phil. Trans. R. Soc. B*, **330**, 351–370.
- CLAYTON, N. S. 1993. Song, sex and sensitive phases in the behavioural development of birds. *Trends Ecol. Evol.*, **4**, 82–84.
- COOKE, F. AND MCNALLY, C. M. 1976. Mate selection and colour preferences in lesser snow geese. *Behaviour*, **103**, 151–170.
- DOBZHANSKY, T. 1940. Speciation as a stage in evolutionary divergence. *Am. Nat.*, **74**, 312–321.
- EMLEN, S. T., RISING, J. D. AND THOMPSON, W. L. 1975. A behavioral and morphological study of sympatry in the Indigo and Lazuli Buntings of the Great Plains. *Wilson Bull.*, **87**, 145–302.
- FABRICIUS, E. 1991. Interspecific mate choice following cross-fostering in a mixed colony of Greylag Geese (*Anser anser*) and Canada Geese (*Branta canadensis*): a study on development and persistence of species preferences. *Ethology*, **88**, 287–296.
- FEAR, K. K. AND PRICE, T. 1998. The adaptive surface in ecology. *Oikos*, **82**, 440–448.
- FELSENSTEIN, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution*, **35**, 124–138.
- GERHARDT, H. C. 1994. Reproductive character displacement of female mate choice in the grey treefrog, *Hyla chrysoscelis*. *Anim. Behav.*, **47**, 959–969.
- GIL, D. 1997. Increased response of the short-toed tree creeper *Certhia brachydactyla* in sympatry to the playback of the song of the common treecreeper *C. familiaris*. *Ethology*, **103**, 632–641.
- GILL, F. B. AND MURRAY, B. G. JR. 1972. Discrimination behavior and hybridization of the Blue-winged and Golden-winged warblers. *Evolution*, **26**, 282–293.
- GRANT, P. R. 1986. *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton, NJ.
- GRANT, B. R. AND GRANT, P. R. 1996. High survival of Darwin's finch hybrids: effects of beak morphology and diets. *Ecology*, **77**, 500–509.
- GRANT, P. R. AND GRANT, B. R. 1997a. Hybridization, sexual imprinting, and mate choice. *Am. Nat.*, **149**, 1–28.
- GRANT, P. R. AND GRANT, B. R. 1997b. Genetics and the origin of bird species. *Proc. Natl. Acad. Sci. U.S.A.*, **94**, 7768–7775.
- GRANT, B. R. AND GRANT, P. R. 1998. Hybridization and speciation in Darwin's finches: the role of sexual imprinting on a culturally transmitted trait. In: Howard, D. J. and Berlocher, S. L. (eds) *Endless Forms: Species and Speciation*, pp. 404–422. Oxford University Press, Oxford.
- HALPIN, Z. T. 1991. Kin recognition cues of vertebrates. In: Hepper, P. G. (ed.) *Kin Recognition*, pp. 220–259. Cambridge University Press, Cambridge.
- HARRIS, M. 1970. Abnormal migration and hybridization of *Larus argentatus* and *L. fuscus* after interspecies fostering experiments. *Ibis*, **112**, 488–498.
- HINDE, R. A. 1961. The establishment of the parent-offspring relationship in birds with some mammalian analogies. In: Thorpe, W. and Zangwill, O. (eds) *Current Problems in Animal Behaviour*, pp. 175–193. Cambridge University Press, Cambridge.
- HINDE, R. A. 1962. Some aspects of the imprinting problem. *Symp. Zool. Soc. Lond.*, **8**, 129–138.
- HONEY, R. C., BATESON, P. AND HORN, G. 1994. The role of stimulus comparison in perceptual learning: an investigation with the domestic chick. *Q. J. Exp. Psych. B*, **47**, 83–103.
- HOWARD, D. J. 1993. Reinforcement: origin, dynamics, and fate of an evolutionary hypothesis. In: Harrison, R. G. (ed.) *Hybrid Zones and the Evolutionary Process*, pp. 46–69. Oxford University Press, Oxford.
- IMMELMANN, K. 1972. Sexual and other long-term aspects of imprinting in birds and other species. *Adv. Stud. Behav.*, **4**, 147–174.
- IMMELMANN, K. 1975. Ecological significance of imprinting and early learning. *Ann. Rev. Ecol. Syst.*, **6**, 15–37.
- KENDRICK, K. M., HINTON, M. R., ATKINS, K., HAUPT, M. A. AND SKINNER, J. D. 1998. Mothers determine sexual preferences. *Nature*, **395**, 229–230.
- KENT, J. P. 1987. Experiments on the relationship between the hen and chick (*Gallus gallus*): the role of auditory mode in recognition, and the effects of maternal separation. *Behaviour*, **102**, 1–14.
- KIM, Y. K., KOEPPER, H. R. AND EHRMAN, L. 1996. Developmental isolation and subsequent adult behavior of *Drosophila paulistorum*. 3. Alternative bearing. *Behav. Genet.*, **26**, 27–37.
- KRUIJT, J. P., BOSSEMA, I. AND LAMMERS, G. J. 1982. Effects of early experience and male activity on mate choice in mallard females (*Anas platyrhynchos*). *Behaviour*, **80**, 32–43.
- LALAND, K. N. 1994. On the evolutionary consequences of sexual imprinting. *Evolution*, **48**, 477–489.
- LIU, L. W. AND PRICE, T. D. 1994. Speciation by reinforcement of premating isolation. *Evolution*, **48**, 1451–1459.
- LORENZ, K. 1937. The companion in the bird's world. *Auk*, **54**, 245–273.
- LYNCH, A. AND BAKER, A. J. 1990. Increased vocal discrimination by learning in sympatry in two species of chaffinches. *Behaviour*, **116**, 109–126.
- MARTENS, J. 1996. Vocalizations and speciation of Palearctic birds. In: Kroodsma, D. E. and Miller, E. H. (eds) *Ecology and Evolution of Acoustic Communication in Birds*, pp. 221–240. Cornell University Press, Ithaca.
- MAYR, E. 1970. *Populations, Species, and Evolution*. Belknap Press of Harvard University Press, Cambridge, MA.
- MORRISON, M. L. 1982. The structure of western warbler assemblages: ecomorphological analysis of the Black-throated Gray and Hermit warblers. *Auk*, **99**, 503–513.
- NOOR, M. A. 1995. Speciation driven by natural selection in *Drosophila*. *Nature*, **375**, 674–675.
- NOOR, M. A. F. 1997. How often does sympatry affect sexual isolation in *Drosophila*? *Am. Nat.*, **149**, 1156–1163.
- NUECHTERLEIN, G. L. 1981. Courtship behavior and reproductive isolation between western grebe color morphs. *Auk*, **98**, 335–349.
- NUECHTERLEIN, G. L. AND BUITRON, D. 1998. Interspecific mate choice by late-courting male western grebes. *Behav. Ecol.*, **9**, 313–321.
- OETTING, S., PROVE, E. AND BISCHOF, H. J. 1995. Sexual imprinting as a two-stage process: mechanisms of information storage and stabilization. *Anim. Behav.*, **50**, 393–403.
- PRESCOTT, D. R. C. 1987. Territorial responses to song playback in allopatric and sympatric populations of Alder (*Empidonax alnorum*) and Willow (*E. traillii*) flycatchers. *Wilson Bull.*, **99**, 611–619.
- PRICE, T. 1998. Sexual selection and natural selection in bird speciation. *Phil. Trans. R. Soc. B*, **353**, 251–260.
- RATCLIFFE, L. M. AND GRANT, P. R. 1983. Species recognition in Darwin's finches (*Geospiza*, Gould). II. Geographic variation in mate preference. *Anim. Behav.*, **31**, 1154–1165.
- RICE, W. R. AND HOSTERT, E. E. 1993. Laboratory experiments on speciation: What have we learned in 40 years? *Evolution*, **47**, 1637–1653.

- RICE, W. R. AND SALT, G. W. 1990. The evolution of reproductive isolation as a correlated character under sympatric conditions: experimental evidence. *Evolution*, **44**, 1140–1152.
- RUNDLE, H. D. AND SCHLUTER, D. 1998. Reinforcement of stickleback mate preferences: Sympatry breeds contempt. *Evolution*, **52**, 200–208.
- SCHIMMEL, L. AND WASSERMAN, F. 1991. An interspecific comparison of individual and species recognition in the Passerines *Turdus migratorius* and *Cyanocitta cristata*. *Behaviour*, **118**, 115–126.
- SEIGER, M. B. 1967. A computer simulation study of the influence of imprinting on population structure. *Am. Nat.*, **101**, 47–57.
- SPALDING, G. S. 1873. Instinct, with original observations on young animals. *Macmillan's Mag.*, **27**, 282–293.
- TEMELES, E. J. 1994. The role of neighbours in territorial systems: When are they 'dear enemies'? *Anim. Behav.*, **47**, 339–350.
- TENCATE, C., VOS, D. R. AND MANN, N. 1993. Sexual imprinting and song learning; two of one kind? *Neth. J. Zool.*, **43**, 34–45.
- VOS, D. R. 1995. The role of sexual imprinting for sex recognition in zebra finches: a difference between males and females. *Anim. Behav.*, **50**, 645–653.
- WADDINGTON, C. H. 1953. Genetic assimilation of an acquired character. *Evolution*, **7**, 118–126.
- WADDINGTON, C. H. 1959. Canalization of development and genetic assimilation of acquired characters. *Nature*, **183**, 1654–1655.
- WARRINER, C. C., LEMMON, W. B. AND RAY, T. S. 1963. Early experience as a variable in mate selection. *Anim. Behav.*, **11**, 221–224.
- WCISLO, W. T. 1989. Behavioral environments and evolutionary change. *Ann. Rev. Ecol. Syst.*, **20**, 137–169.