

## S18-3 Causes of post-mating reproductive isolation in birds

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**Abstract** Speciation involves the establishment of both pre-mating and post-mating reproductive isolation between divergent populations. Post-mating barriers have been particularly difficult to study in birds. I review what is known about three main forms of post-mating isolation. The first, intrinsic genetic incompatibility, reflects hybrid infertility and inviability independent of the environment in which the hybrids are found. They can be studied using data from captive breeding experiments. Results suggest that incompatibilities imposing complete reproductive isolation often arise after the speciation process has been completed. The second, ecological selection against hybrids, results from environmental conditions and/or competition from parental types and has been demonstrated on a few occasions. The third, sexual selection against hybrids, which arises from mate preferences for one or other parental species, may be an important, relatively neglected post-mating isolation process. Hybrid males often show characteristics intermediate to the parental species, and have unusual displays. Some experiments have demonstrated that females show weaker sexual responses to courting hybrid males. Several field studies have implicated both female choice and competition among males for territories in causing hybrid unfitness. Ecological and behavioral causes of post-mating isolation may play a major role in speciation but present evidence is too limited to evaluate their importance.

**Key words** Hybrids, Natural selection, Pre-mating isolation, Reproductive isolation, Sexual selection, Speciation

### 1 Introduction

Species remain distinct ultimately because of a lack of genetic exchange between them. Genetic interchange can be cut off both through barriers at the pre-mating (e.g., mate choice) stage or at the post-mating stage. Post-mating barriers include the failure of the sperm to fertilize the egg, the failure of eggs to develop, and the inviability and infertility of hybrids. Most individuals of a species mate with conspecifics (Kirkpatrick and Ravigné, 2002), which implies that complete speciation may result from divergence in traits used in pre-mating reproductive isolation. For example, models of sexual selection have shown how correlated evolution of sexually selected traits and preferences for those traits can result in individuals from one population failing to recognize individuals from another as suitable mates (reviewed in Price, 1998).

While speciation may arise from pre-mating isolation alone, three lines of evidence suggest that post-mating isolation is usually involved as well, and may be critical to it. First, hybridization among species does occur (Panov, 1989). There are several examples of hybrid zones where hybridization is common, yet species each side of the hybrid zone remain distinct (Moore and Price, 1993). Almost 10% of all bird species have been recorded hybridizing in nature (Grant and Grant, 1992). Although many of these hybridization events are based on one or a few records they imply that rates of hybridization are at least comparable with mutation rates, and suggest that a gradual merging of species would happen unless prevented by lowered fitness in hybrids.

Secondly, post-mating isolation is integral to the model of speciation based on reinforcement of mating preferences (Dobzhansky, 1940; Noor, 1999). In this model, increased levels of pre-mating isolation result from selection to avoid mating with heterospecifics, specifically because hybrids are unfit. There is some evidence for reinforcement in nature (Howard, 1993; Sætre et al., 1997), and theoretical models show reinforcement to be a likely outcome whenever hybrid fitness is very low (Liou and Price, 1994). Reinforcement may often result from the refinement of mate recognition rather than divergence in traits used for recognition (Ratcliffe and Grant, 1983; Irwin and Price, 1999). Although not quantified, it does appear that very small differences between species occasionally form the basis of strong mate recognition. It seems unlikely that these differences would be sufficient for pre-mating isolation to have evolved entirely as a correlated response of the mate recognition system to the traits that distinguish the species, without some reinforcement of the recognition process. For example, two species of chiffchaffs *Phylloscopus collybita* and *P. sindianus* singing similar songs and with similar plumages coexist in sympatry in the Caucasus, apparently without hybridizing (Martens, 1996).

The third line of evidence implicating post-mating isolation in speciation comes from examples of hybridizing species where hybrid fitness has been measured and found to be low (e.g., Lanyon, 1979; Veen et al., 2001). Pre- and post-mating barriers seem to have accumulated between these species at a comparable rate.

In this paper I review causes of post-mating isolation in birds. These fall broadly into three categories (Coyne and Orr, 1998; Table 1), although there is overlap between them. The first is that of intrinsic genetic incompatibility: hybridization events result in no offspring or offspring with reduced fertility, defects that are independent of the environment. The second is that of hybrids with reduced fitness because they fall between the ecological niches of the parental types, and the third is that of hybrids which are unable to attract mates. Not very much is known about the latter two forms of unfitness, and they are a major gap in our understanding of speciation. It is maintained here that sexual selection against hybrids is an important form of post-mating reproductive isolation.

## 2 Intrinsic incompatibilities

Sexual conflict, i.e. the different interests of males and females, can result in the rapid evolution of genes affecting fertility, leading to the development of reproductive isolation between populations (Rice, 1998). First, sperm may fail to fertilize. While this may be important (Price et al., 2001), it has not been explicitly demonstrated as a cause of infertility in bird crosses. A second prediction of the sexual conflict model is that fertility problems in hybrids should arise much more frequently than viability problems (Rice, 1998). This expectation is born out (Price and Bouvier, 2002). Comparisons among species crossed in captivity indicate that hybrids are regularly produced but often show reduced fertility (Price and Bouvier, l.c.). Hybrid infertility may arise from problems of chromosome pairing at meiosis (Smith and Thomas, 1913; Mott et al., 1968), as well as genetic interactions.

The relatively rapid development of infertility implies that if intrinsic incompatibility contributes to post-mating isolation, it will be due to hybrid infertility rather than inviability. In fact, complete loss of hybrid fertility seems to take a long time (Price and Bouvier, 2002). A classic example is the mallard (*Anas platyrhynchos*) and pintail (*Anas acuta*), which may have diverged > 4 MYA (Price and Bouvier, 2002) yet still produce fully fertile hybrid offspring (Sharpe and

Johnsgard, 1966). More than half of all studied crosses between congeneric species produce fully fertile offspring (Price and Bouvier, 2002). This number is biased but it does suggest that the contribution of intrinsic incompatibility to speciation is often small.

There are several caveats. First, the timescale for at least partial loss of fertility is of the same order as that for speciation in some pairs of species. In particular, hybrid females may have reduced fertility, or even be infertile, even though males are not (Price and Bouvier, 2002). For example, female hybrids of two flycatchers (*Ficedula* spp.), which may have been separated by about 2 million years (Price and Bouvier, 2002), are infertile (Veen et al., 2001). A second caveat is to be found in the appearance of intrinsic incompatibilities in the F2 or backcross generations rather than the F1 because many of the deleterious effects of gene combinations appear to be recessive (Turelli and Orr, 2000). There are few records in ornithology where fertile F1s have been taken through either the F2 or backcross generations. Thus in the European and Japanese quail, *Coturnix* spp. (Deregnacourt et al., 2002) and the mallard and pintail (Sharpe and Johnsgard, 1966), both F1s and F2s appear to be fully fertile. But in crosses between the gray and red junglefowl (*Gallus* spp.), the F1s show some reduced fertility with respect to parental species; and in the F2s fertility is much lower still (Morejohn, 1968).

## 3 Ecological selection

Hybrids may be unfit because they fall between the ecological niches of parental species. Moore (1977) and Moore and Price (1993) argued that many hybrid zones were areas of “bounded hybrid superiority”, where hybrid fitness was equal to or higher than parental fitness within the zone but lower outside it, as a consequence of spatially varying environmental conditions. Moore and Price (1977) demonstrated correlations of the spatial distributions of the hybridizing forms with several climatic and biotic variables to bolster the case.

So-called migratory divides provide more direct examples of situations where hybrids are likely to be unfit

**Table 1** Types of post-mating isolation in birds, citing the most recent reviews

Category	Sub-category	Most recent review
Intrinsic genetic incompatibility	*Post mating, pre zygotic	—
Intrinsic genetic incompatibility	Hybrid inviability	Price and Bouvier, 2002
	Hybrid infertility	Price and Bouvier, 2002
	F2 and backcross breakdown	This paper
Ecological selection	Feeding	Grant and Grant, 1996
	Migratory direction divides	Irwin and Irwin, 2003
	Migratory distance divides	Rohwer and Manning, 1990
Reproductive selection	Nest building	Buckley, 1969
	Sexual selection	Price, 2002; this paper

\*Although this sub-category may be important, it has not been studied in birds; a brief review of the phenomenon is given in Price et al. (2001).

(Helbig, 1991; Irwin and Irwin, 2004). If two species migrate along different routes, the hybrids may migrate along an intermediate course and have lower fitness as a consequence. Helbig (1991) conducted a captive breeding experiment on the blackcap, *Sylvia atricapilla*, which has SW and SE migrating populations, and showed that hybrids take up an intermediate orientation. Irwin and Irwin (2004) review comparative studies. They show that different subspecies of a number of Siberian species migrate to southern Asia around west or east sides of the Tibetan plateau, which infers that hybrids between two such subspecies might migrate due south across the plateau, with correspondingly reduced fitness. Migratory divides in Siberia are a good illustration of how low hybrid fitness can arise out of gradual divergence among populations: migration orientation is likely to have changed gradually as populations spread from ancestral areas (Irwin and Irwin, 2004).

In a somewhat parallel situation are the many examples of closely related taxa that include both resident and migratory members. Cross-breeding experiments among resident and migratory populations of the blackcap have shown migratory propensity to be genetic and hybrids to be intermediate (Berthold and Querner, 1981). Harris et al. (1978) showed that hybrids of herring (*Larus argentatus*) and lesser black backed (*L. fuscus*) gulls in Britain did not survive well. Although the causes are unknown, the herring gull is generally resident and the lesser black backed migratory, traits that seem to be at least partly genetic. Cross-fostered lesser black backed migrated normally, but cross-fostered herrings showed some tendency to migrate, although not as far as black backed (Harris, 1970). Rohwer and Manning (1990) and Rohwer and Johnson (1992) argued that unusual migration and associated molt patterns could lower fitness in hybrid Baltimore and Bullock's orioles (*Icterus galbula galbula* and *I. g. bullocki* respectively). Molt differences may affect hybrids of resident populations too. Gwinner and Neusser (1985) showed that differences among subspecies of African and European stonechats (*Saxicola torquata*) in timing and duration of molt were genetic and intermediate in hybrids.

Measurements comparing hybrid and parental fitness in migration and molt have yet to be taken, but some are available for foraging. Hybrids in Darwin's finches, *Geospiza* spp. (Grant and Grant, 1996) are intermediate in morphology and have diets intermediate between those of parental species, with demonstrable consequences for hybrid fitness (Grant and Grant, 1996). Good et al. (2000) found that hybrid gulls (*Larus* spp.) exhibited the habitat preferences of one species in one area, and the diet of the other in another area, both of which influenced fitness. The flipside of differences in fitness between hybrids and parental taxa in foraging is an association of similar fitnesses with similar foraging among hybrids and parentals, as appears to be the case in a gull hybrid zone (Ingolfsson, 1970).

It is common to find hybridizing species associated with distinct habitats and to hybridize only where those

habitats meet (e.g., Yang and Selander, 1968; Saino, 1992; Saino and Villa, 1992). Hybrid wagtails *Motacilla flava* (Sammalisto, 1968) and crows *Corvus corone* (Saino, 1992) have more catholic habitat preferences than parental taxa, although whether these preferences affect fitness is unknown. In the wagtails, however, Sammalisto (1968) found a strong correlation across years between the proportion of hybrids and temperature during the nestling period of the previous year.

## 4 Sexual selection

In birds, species recognition is attributable largely to imprinting, whereby offspring learn the characteristics of their parents and use these characteristics in mating decisions (ten Cate and Vos, 1999; ten Cate, this symposium). Imprinting on habitat may also happen (reviewed in Teuschl et al., 1998). If hybrids look or sound different from either parent, or occur in a different habitat, they may obtain mates less readily, because parental types ignore them. In addition, hybrid females may retain preferences for the parental species that raised them, rather than for hybrid males. Female zebra finches (*Taeniopygia guttata*) learn characteristics of their father's song and respond sexually to similar songs (Clayton, 1990). Male hybrids between the two subspecies of zebra finch sing songs different from either parental species and females of both parental types respond weakly to them (Fig. 1). Hybrid females do respond to songs produced by hybrid males, but they respond even more strongly to songs resembling the male that reared them (Fig. 1). In other species, hybrids may sing songs closely resembling the paternal type but differ instead in other sexually selected traits, including courtship and plumage pattern (Price, 2002). Conversely, in natural situations where hybridization is frequent, the parental taxa and hybrids are alike in at least some of these features, including voice and display (Yang and Selander, 1968), and coloration and display (Grant and Grant, 1997).

In many hybrid zones there is strong assortative mating (Jiggins and Mallet, 2000), parental types pairing with each other (Saino and Villa, 1992; Sætre et al., 1999; Grant and Grant, 1997). Hybrids also obtain mates, but it is not known how often assortative mating translates into sexual selection against them; in Darwin's finches it is thought not to (Grant and Grant, 1997). In other hybrid zones, moreover, mating is random (Ingolfsson, 1970; Moore, 1987; Good et al., 2000). Observations of random mating do not necessarily imply an absence of sexual selection against hybrids. Based on experimental manipulations of color patterns by Nobel (1936), Moore (1987) argues that an important component of selection against hybrid flickers is male competition for territories: male hybrids outside the hybrid zone are less able to establish themselves because their unusual color patterns give a less effective signal.

Quantitative measurements of sexual selection against hybrids are as rare as measurements of ecological selection. In *Vermivora* warblers, hybrid males had only 60% of the

pairing success of parental males (Ficken and Ficken, 1968); and in two sister grebe species (*Aechmophorus* spp.), early season pairing success among hybrids was 30% of that of the common parental type (Neuchterlein and Buitron, 1998). Pearson (2000) studied territory maintenance and pairing success in two *Dendroica* warblers; hybrid males had success much as in one parental species and about 75% of the success in the other. Moore and Koenig (1986) also found that hybrid flicker males had smaller broods than the parental species. They raised the interesting possibility that females paired with hybrids were less stimulated and hence put less effort into reproduction.

## 5 Discussion

Results from captive breeding experiments suggest that intrinsic barriers imposing post-mating isolation may be weak among closely related species. Directly assessing ecological and behavioral causes of hybrid unfitness in the field, moreover, is very difficult and there are few thorough studies (Jiggins and Mallet, 2000). The difficulties are that hybrids are often rare and that measurements of selection in general are not easy, because individuals may need to be followed through their lifetime.

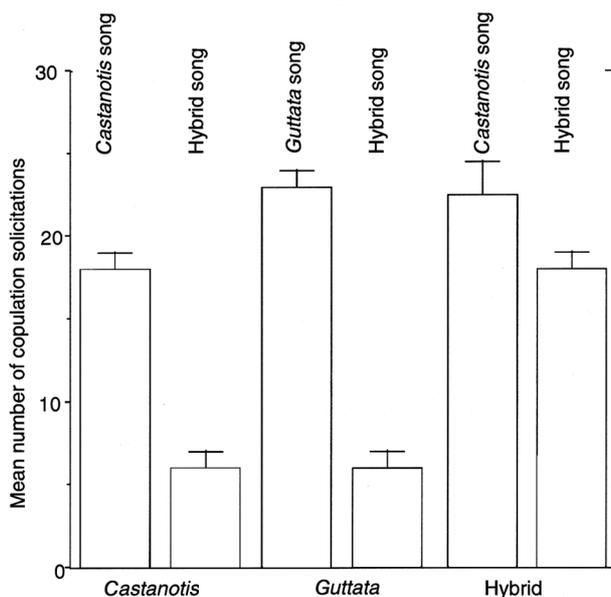
Hybrids may suffer reduction in fitness from multiple causes. Thus in the crow hybrid zone studied by Saino (1992), behavioral observations suggest the possibility of forms of both sexual and ecological selection against hybrids. Moreover, egg volume, chick survival and number

of chicks fledged per nest were all lower in hybrid females than the parental types (Saino and Bolzern, 1992; Saino and Villa, 1992); and some hybrid females laid abnormal, thin-shelled eggs (Saino and Villa, 1992). Hybrid females between collared and pied flycatchers are infertile (Veen et al., 2001). Assortative mating within the hybrid zone (Sætre et al., 1999) raises the possibility of sexual selection against hybrids; and there may also be ecological selection imposed by habitat choice and migratory differences (Veen et al., 2001).

Because natural selection can generate rapid evolution, ecological causes of post-mating isolation may precede the development of intrinsic genetic incompatibilities. This is especially likely in the early stages of an adaptive radiation, characterized by rampant divergent natural selection (Schluter, 2000). But the very long time that it takes to produce genetic incompatibilities implies that the ecological conditions that promoted both divergence and associated post-mating barriers must persist for a very long time if species are to become a permanently reproductively isolated through the build up of such incompatibilities. Thus Grant and Grant (1992, 1996) showed that even if foraging differences between hybrid and parental species of Darwin's finches impose a post-mating barrier, the barrier disappears following years of abnormally high rainfall and associated changes in resource distribution. In such years, hybrids had higher survival than at least one of the parental species. Such inconsistency with the ecological barrier hypothesis may be explained by divergence along multiple ecological dimensions (prey, habitat, feeding method, nest site etc.); all dimensions are unlikely to collapse at the same time. Rice and Hostert (1993) noted the importance of multiple dimensions in their review of selection experiments promoting reproductive isolation.

The possibility that sexual selection against hybrids contributes to post-mating isolation has been relatively neglected, even though hybrid males have often been recorded as having difficulties in courtship (Sharpe and Johnsgard, 1966; Price, 2002). It is possible that an unusual hybrid will sometimes be favored more under sexual selection than either parental species, leading to a new 'hybrid' species. There is little evidence that this has ever happened in birds (Price, 2002). Sexual selection against hybrids is expected to act predominantly against males and therefore is unlikely to impose complete post-mating isolation. However, intrinsic hybrid unfitness arises first in female hybrids (Haldane's rule), and should complement any loss of fitness in males due to sexual selection (Price and Bouvier, 2002, for birds).

Sexual selection against hybrids may be less affected by altered conditions than ecological causes of hybrid unfitness. In addition, related species usually differ in multiple sexually selected traits, and may continue to accumulate more differences with time, so hybrids grow increasingly different from both parent species (Price, 2002). Thus Baker and Baker (1990) showed that both song and plumage pattern were involved in mate choice in hybridizing



**Fig. 1** Number of copulation-solicitation displays (+ SD) of estradiol-implanted female zebra finches (*Taeniopygia guttata*) to playback of songs of males of two subspecies and their hybrids

Twelve females from each subspecies (*T. g. castanotis* and *T. g. guttata*) were tested, as were 12 hybrid females that had been raised by *castanotis* females and *guttata* males. Responses were measured to 1) songs of own subspecies, and 2) songs of hybrids between the two subspecies (data from Clayton, 1990).

buntings and that these two traits contributed more or less equally to female response. The implication here is that hybrids mismatched in plumage and song would be disadvantaged.

Sexual selection against hybrids has important consequences for the ease with which reinforcement of pre-mating isolation can work. In the reinforcement model, hybrid unfitness leads to selection favoring divergence in traits used in pre-mating isolation (Howard, 1993; Liou and Price, 1994). The chief theoretical difficulty here is that the traits used in pre-mating isolation may become dissociated from those used in post-mating isolation, as a result of recombination in hybrids (Rice and Hostert, 1993). Sexual selection against hybrids is likely to be based on the same traits that are used in species recognition during mate choice, so that the traits effecting pre-mating isolation also impose some post-mating isolation, at least in males. Kirkpatrick and Servedio (1999) show theoretically how sexual selection against hybrids can lead to a strengthening of mate preferences in an island population, even when other kinds of hybrid unfitness were absent.

The two main conclusions to be drawn from this review are (1) a critical step in speciation is likely to include the generation of post-mating isolation, and (2) sexual selection against hybrids may contribute to this isolation. Even if intrinsically viable and fertile offspring are produced, post-mating isolation is often difficult to study in the field because hybridization events are usually rare. More field studies of hybrid fitness are needed, but much would also be gained from experimental studies of mate choice in the laboratory of the kind foreshadowed by Clayton (1990) and Baker and Baker (1990), both of whom showed weaker female responses to hybrid male courtship traits (Fig. 1).

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