



Reproductive interference via display signals: the challenge of multiple receivers

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Abstract Sexually selected traits important in both mate and competitor recognition provide an opportunity to understand the tradeoffs associated with reproductive and competitive interference. When co-occurring species compete over similar resources, selection may promote signal similarity to facilitate competitive interactions in opposition to selection for signal divergence to maintain assortative mating. Bird song provides a classic example of contrasting selection on signal design, because songs function both in mate discrimination and in territorial advertisement. Similarity in songs aids competitor recognition both within and across species, and song convergence or mixing is widespread in the songbirds. Two related mechanisms can maintain mate recognition in the face of song convergence. First, multiple recognition signals, both across and within signaling modalities, provide a basis for mate and competitor discrimination using different sets of cues. Second, stricter female song preferences may allow interspecific male–male competitive communication without compromising female mate discrimination. I suggest that increased understanding of the neurobiology underlying song recognition will provide insight into the relative importance and prevalence of these different mechanisms along a continuum of species divergence.

Keywords Competitive interference · Evolutionary tradeoffs · Reproductive interference · Song · Sexually selected signals

As highlighted by the articles in this special feature, the prevalence and evolutionary consequences of reproductive interference are becoming increasingly appreciated, but many challenges and ambiguities remain (Gröning and Hochkirch 2008; Kyogoku 2015). One major task is establishing the evolutionary consequences of the different mechanisms of reproductive interference at different stages of species divergence and the degree to which they are likely to persist despite reproductive character displacement (Gröning and Hochkirch 2008; Takakura et al. 2015). This task is especially difficult because the predicted evolutionary effects of reproductive interference may be obscured by other factors, such as ecological competition (Grether et al. 2009; Shuker et al. 2015) or environmental constraints (Weir et al. 2012). Traits important both in mate recognition and male–male competitive contexts connect the processes of reproductive and competitive interference (Grether et al. 2009), thereby offering a tremendous opportunity to study how variation in the relative strength of selection in these different contexts can interact to promote a variety of evolutionary responses (e.g., Hunt et al. 2009). Here, I first outline the ways in which bird song is a model system for investigating the evolutionary consequences of selection in mate attraction and interspecific rivalry. Next, I outline two ways in which song signaling systems accommodate these contrasting selection pressures and suggest that investigating the neural basis of song will provide insight into the evolutionary consequences of reproductive interference.

Mate recognition traits have been long been studied as a potential source of reproductive interference among closely related species (Gröning and Hochkirch 2008), and the costs of pairing with a heterospecific are generally predicted to drive divergence in sexual signals and/or preferences for those signals (Servedio and Noor 2003; Gröning

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and Hochkirch 2008; Hudson and Price 2014). In contrast to this prediction, signals involved in mate attraction often converge where species co-occur (Cody 1969; Helb et al. 1985; Grether et al. 2009; Lackey and Boughman 2013; Tobias et al. 2014). Signal convergence has been especially well documented in the songs of syntopic songbirds (oscine passerines), a phenomenon referred to as mixed singing when convergence occurs through incorporation of typical heterospecific song elements (Helb et al. 1985). One explanation for mixed song is that it is a non-adaptive byproduct of an open song-learning process otherwise promoted by sexual selection on repertoire size (Helb et al. 1985; Secondi et al. 2011; Vokurková et al. 2013). According to this view, a general female preference for elaborated songs overrides any costs to mixing. The generality of mistaken learning as a driver for mixed song is currently unknown (Kelley et al. 2008; Dalziel et al. 2014), but it is unlikely to be the only explanation, as similarly convergent song is also widely found in non-vocal learning bird species (den Hertog et al. 2007; Tobias et al. 2014). These authors and others studying mixed singing in songbird species suggest that song convergence may sometimes be an adaptation to facilitate interspecific competitive interactions (Baptista and Catchpole 1989; Gorissen et al. 2006; Qvarnström et al. 2006; Laiolo 2012). Song is a critical component of male displays over breeding territories and nesting sites and, as a result, having the same song as a heterospecific neighbor has been suggested to facilitate competitive interactions similarly to song-type matching among conspecifics (Rohwer 1973; Catchpole and Slater 1995).

The majority of examples of reproductive interference suggest larger costs on females than males (Gröning and Hochkirch 2008; Kyogoku 2015; Takakura et al. 2015), but mixed singing may lead to the reverse pattern. This is because producing mixed song may directly increase the likelihood that a male invests a breeding event in a costly mixed pairing (Grant and Grant 1997; Qvarnström et al. 2006), while females may be able to alleviate some of the costs by performing extra-pair copulations with males from their own species (Svedin et al. 2008). Given the costs associated with mixed pairing and the evolutionary lability of cultural traits, such as song, we might generally expect mixed singing to be an evolutionary transient state that occurs only very briefly after sympatry (e.g., Haavie et al. 2004) and for males to quickly evolve other methods to negotiate interspecific competition. However, recent comparative studies in non-vocal learning suboscines suggest that convergence can be maintained or even increase over long periods of sympatry (Tobias et al. 2014). Here, I outline two non-mutually exclusive ways in which mate communication systems can accommodate song convergence and mixing, while still maintaining assortative

mating: (1) multiple signal components, and (2) intersexual difference in perceptual systems.

Mate recognition in birds relies not only on song, but on a wider suite of sexual signals, such as plumage patches (Baker and Baker 1990; Uy et al. 2009). Different sexual signals may be directed at males and females (Karubian et al. 2009), suggesting that, despite similarity across species in one signal that promotes interspecific male–male communication, females may be able to rely on additional cues to recognize conspecifics. Bird songs themselves are composed of multiple components and differ along multiple axes of variation, suggesting that, despite widespread song mixing, at least some song features are likely to vary across species (Reichard and Price 2008). Male singers also may emphasize particular song components during interactions with conspecific males, allowing different components within the same song to communicate with different audiences (e.g., chaffinches, *Fringilla coelebs*, Leitão and Riebel 2003; blackcaps, *Sylvia atricapilla*, Leedale et al. 2015). I suggest that interactions with heterospecifics can be accommodated in the same way. For example, if males from one species use certain song components during intraspecific competitive interactions, it is likely they will also use those components during competitive interactions with males from another species. As a result, it is exactly those components that are likely to be learned by heterospecific males, meaning that songs may be more likely to mix only those elements directed at males, while maintaining species specificity in song components directed at females. This hypothesis predicts that those song features directed at males should be more similar across species than those directed at females, but this remains untested.

Differences in perceptual specificity across males and females may allow mate discrimination despite highly convergent signals across species. Experiments on a wide variety of avian species, both vocal learners and non-learners, have demonstrated that males respond to a wider range of songs than do females (Searcy and Brenowitz 1988; Searcy 1990; Searcy et al. 1997; Nelson and Soha 2004; Nowicki and Searcy 2004; Seddon and Tobias 2010; Danner et al. 2011; Curé et al. 2012). Stricter female song discrimination compared to that of males could allow competitor recognition through song convergence in sympatry, while maintaining species-specific mate recognition (Fig. 1). For example, the songs of a pair of *Hypocnemis* ant bird species are highly similar where they co-occur, which is suggested to be a result of social selection to recognize ecologically similar competitors (Tobias and Seddon 2009). Females retain the ability to discriminate potential mates from each species through more stringent song preferences than males (Seddon and Tobias 2010). A recent meta-analysis suggested that divergence in female

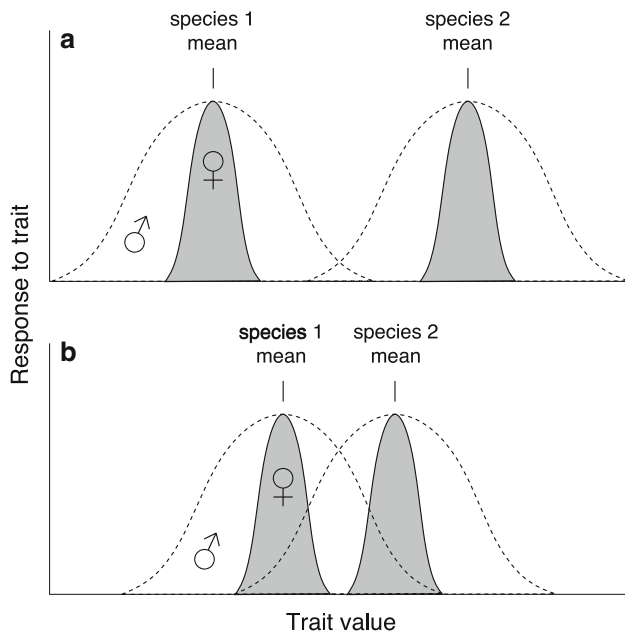


Fig. 1 Response curves of males (unshaded regions bounded by a dashed lines) and females (shaded regions bounded by solid lines) from two species to a sexually selected signal along an axis of trait variation. **a** Little overlap between preferences of males or females. **b** Male–male agonistic interactions may select for signal convergence. As long as female preference curves are narrower than those for males, substantial overlap in male preferences can occur without overlap in female preferences

song preferences across species may be more likely to maintain species discrimination than acoustic divergence in songs themselves (Hudson and Price 2014), which may be especially likely when the songs of co-occurring species converge (Tobias et al. 2014).

Song learning depends on a suite of specialized regions in the songbird forebrain, found in both male and female birds, in which auditory memories are formed and stored (i.e., the song system, Nottebohm and Liu 2010; Bolhuis and Moorman 2015). Species-specific biases in the types of songs learned and ultimately preferred as adults are driven by innately determined variation in the development and regulation of genes involved in neural plasticity in these regions (Marler 1997; Adret 2004; Bolhuis and Moorman 2015). The volume of song system nuclei has been shown to correlate with male song repertoire size across species (i.e., the average number of unique songs sung, DeVoogd et al. 1993) and to the plasticity of the song learning process in the Bengalese finch and its wild progenitor, the white-rumped munia, *Lonchura striata* (Okanoya 2006). These results imply that the volume of song brain nuclei influences variation in the types of songs perceived by males as coming from their own species. Female songbirds also learn a range of songs that they perceive as coming from appropriate mates (Hudson and Price 2014), but the

volume of the female song-learning nuclei are significantly smaller across species (Nottebohm and Arnold 1976). This difference has been suggested to lead to a less open song-learning process in females, which may underlie their stricter song preferences (Cynx 1993; Tomaszycski and Blaine 2014). A sexual difference in song learning nuclei provides a mechanism to explain the sexual difference in song preferences, even if it is likely to have evolved as a result of sexual selection for elaborated male song traits (Nottebohm and Liu 2010). A recent review by Odom et al. (2014) suggests that female singing may be much more widely prevalent in the songbirds than is commonly appreciated. An increased understanding of the function and neural substrate of female song may provide additional insight into the evolutionary basis of sex differences in song recognition.

I have suggested two potential mechanisms through which the tradeoffs associated with selection promoting interspecific competition and selection to reduce reproductive interference can be accommodated—multiple signal components and strict female preferences. However, it is likely that these mechanisms, as well as additional ones, act synergistically. For example, some studies have demonstrated that females pay attention to more song components than males, which may make it even easier for them to pick out and, thereby, focus on any discriminating features (Curé et al. 2012). As a result, it may be unlikely for song similarity to directly promote mixed mating, precisely because song is generally so important for mate recognition and because female preference windows are expected to rapidly become stricter in sympatry (Hudson and Price 2014). Song similarity leading to heterospecific pairing is most likely to occur in those occasions when secondary contact arises relatively quickly after speciation, in which case it may have important consequences for the outcome of species interactions (Grant and Grant 1997; Qvarnström et al. 2006). It is here that tradeoffs imposed by competitive and reproductive interference on song learning programs may promote evolutionary responses in neural structures underlying song acquisition in males and females, such as narrower or broader song preferences. Any evolutionary responses are likely to be driven by variation in the genes influencing the development and plasticity of the song system (Adret 2004; Okanoya 2006; Bolhuis and Moorman 2015), implying that understanding the evolutionary causes of reproductive and competitive interference requires an increased understanding of the neuro-genetic basis of species-specific song learning programs.

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