Magic cues versus magic preferences in speciation

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Abstract

Question: How does divergent natural selection lead to divergence in mating traits and the evolution of reproductive isolation?

Background: Ecological speciation of non-allopatric taxa usually requires the evolution of an association between selective mating and the traits underlying ecological adaptation. 'Magic traits' affect both ecological fitness and assortative mating and may therefore mediate rapid evolution of reproductive isolation.

Problem: When assortative mating is mediated by separate preferences and cues, as opposed to being based on trait similarity (e.g. assortment by body size or habitat), pre-mating reproductive isolation between non-allopatric populations often requires divergence in both mating preferences and mating cues. Yet, most proposed cases of magic trait speciation rely on observation of divergent mating cues alone, leaving the consequences for reproductive isolation uncertain.

Solution: We propose that a distinction should be made between mating cues and mating preferences when documenting divergent natural selection on mating traits. We argue that immediate effects of ecological adaptation on mating preferences, through direct selection or through pleiotropy, will drive divergence in both preferences and traits much more predictably than ecological selection on mating cues. The distinction between 'magic cues' and 'magic preferences' is critical for evaluating the evolutionary consequences of divergent selection on mating traits, and implies a need for increased research effort into documenting variation in mating preferences in diverging taxa.

Magic trait speciation

An emerging focus of current speciation research is the quest for 'magic traits': traits that are subject to divergent selection and at the same time mediate selective mating, effectively translating divergent adaptation into reproductive isolation - provided that the trait polymorphism is determined by a single gene (Gavrilets, 2004; Maan and Seehausen, 2011; Servedio *et al.*, 2011; Smadja and Butlin, 2011; Butlin *et al.*, 2012; Norvaišas and Kisdi, 2012; Servedio and Kopp, 2012). Because a single trait, controlled by a single gene, determines both adaptation and mate choice, magic trait speciation does not depend on the build-up and maintenance of linkage disequilibrium between initially independently segregating genes, allowing rapid speciation that is robust to the effects of gene-flow and recombination.

Several recent reviews have provided systematic evaluations of magic trait scenarios. These conclude that pleiotropic effects of divergent adaptation on assortative mating may be more common than is implied by the term 'magic'. However, different kinds of magic traits can be distinguished, and their predicted contributions to reproductive isolation are very different (Servedio *et al.*, 2011; Smadja and Butlin, 2011; Servedio and Kopp, 2012). For example, some magic traits may be trivial, because they are subject to only weak divergent selection, exert only limited influence on non-random mating, or rely on an incomplete link between these two (Haller *et al.*, 2012; Servedio *et al.*, 2012). Here, we aim to highlight another important distinction, namely that between 'magic cues' and 'magic preferences', which we think is underappreciated in the current literature.

Problem

Perhaps the least controversial magic traits are those that control the time or place of reproduction (Rosenzweig, 1995; Kirkpatrick and Ravigné, 2002). With these 'automatic' magic traits (Servedio *et al.*, 2011), divergence in reproductive ecology immediately contributes to reproductive isolation, simply because divergent genotypes no longer meet. Examples include flowering time in plants (Hall and Willis, 2006; Savolainen *et al.*, 2006), host preference in phytophagous insects (Feder *et al.*, 1994; Hawthorne and Via, 2001) and differentiation by water depth in fish (Seehausen and Magalhaes, 2010; Ingram, 2011).

However, in many animal taxa assortative mating is mediated by separate (female) mating preferences and (male) mating cues that initially segregate independently. Divergence in one of these will not automatically lead to reproductive isolation and some may argue that in these cases there can be no 'magic' at all. However, there may still be pleiotropic effects of ecological adaptation on preferences or cues, and these effects are expected to drive trait evolution and divergence considerably faster than indirect selection emerging from variation in offspring fitness.

Unfortunately, most or even all hypothesised cases of non-automatic magic trait speciation in nature are based on observations of divergence in mating cues. For example, divergence in the warning coloration of *Heliconius* butterflies and *Dendrobates* poison frogs may reduce gene-flow between populations, if these colours not only determine predation risk but also affect mate attraction (Summers *et al.*, 1999; Jiggins *et al.*, 2001). Such scenarios require, however, that variation in mating cues somehow translates into variation in mate pair formation, i.e. through differential attraction of different preference genotypes. In other words, whenever selective mating is not driven by one-allele mechanisms such as phenotype matching or imprinting, assortative mating requires

the evolution of divergent preferences as well as divergent cues, and genetic coupling between them.

These are not trivial requirements. Empirical evidence suggests that the evolutionary conservation of ancestral mate preferences, despite population divergence in mating cues, may be common (Ellers and Boggs, 2003; Schwartz and Hendry, 2006; Labonne and Hendry, 2010; Maan and Seehausen, 2011). Also in experimental evolution studies, selection on male ornaments does not always lead to concomitant changes in female preferences (e.g. see Hall *et al.*, 2004 vs. Houde, 1994). This is consistent with the general conclusion, emerging from many theoretical studies, that sexual selection may prevent ecological speciation (Kirkpatrick and Nuismer, 2004; Otto *et al.*, 2008; Pennings *et al.*, 2008). The current focus on magic mating cues obscures this difficulty.

Solution

We propose that a much more powerful interaction between natural and sexual selection arises when divergent adaptation affects mating preferences rather than mating cues. This is because mating cues will then be directly sexually selected to respond to divergence in mating preferences, creating the required genetic coupling of preference and cue (Figure 1).

To the contrary, the effect of divergence in mating cues on preference evolution is less easily predicted because sexual selection on mating preferences is indirect. That is, preference evolution is driven by fitness differences between offspring produced with preferred and unpreferred mates, rather than the fitness of the choosy individual itself. Reproductive isolation between divergently adapting populations then requires the build-up of linkage disequilibrium between the genes under divergent selection and those underlying selective mating – essentially taking the 'magic' out of speciation. Indeed, the strength of indirect selection on mate preferences has been estimated to be an order of magnitude smaller than that of direct selection (Kirkpatrick and Barton, 1997), can be negligible in natural populations (Qvarnstrom *et al.*, 2006), and we expect that it may decay as mating cues approach fixation (Figure 1).

Some preference-determining mechanisms circumvent the problem of indirect selection. For example, imprinting on paternal mating cues immediately translates cue divergence to preference divergence. This is a one-allele mechanism, in which reproductive isolation does not require the spread of two different preference allleles in diverging populations (Felsenstein, 1981; Verzijden *et al.*,). Another exception occurs when the genes for preferences and cues are physically or pleiotropically linked, essentially generating a similarity-based mating system. This may happen in *Heliconius* butterflies, in which mate preference loci are in close physical linkage with wing pattern loci (Kronforst *et al.*, 2006; Chamberlain *et al.*, 2009) – although it is conceivable that this linkage evolved after colour divergence, driven by indirect selection for colour-assortative mating (Merrill *et al.*, 2011). The latter scenario would represent a case in which speciation is not truly magic, but facilitated by the involvement of one magic ingredient, i.e. ecologically-driven divergence in mating cue. However, for all those cases in which preferences and cues are determined by independently segregating genetic factors, we expect that divergent ecological selection (or pleiotropic effects) that target mating preferences rather than mating cues should be more powerful in driving the evolution of assortative mating.

Recognition of this distinction warrants re-assessment of the prevalence of magic trait speciation. How many examples do we know of divergent adaptation affecting mating preferences? An often

cited example is divergent sensory drive (e.g. in stickleback (Boughman, 2001) and cichlid fish (Seehausen *et al.*, 2008)). The current evidence however does not yet discriminate between pleiotropy and indirect selection scenarios, that involve either magic mating cues (i.e. colour signals that diverge in response to heterogeneous visual environments), or non-magic mating cues (i.e. colour signals as arbitrary markers of local adaptation). This is because a direct link between sensory adaptation and female preferences has not been established in either model system (Maan and Seehausen, 2011). In general, convincing evidence for direct effects of divergent ecological selection on mating preferences is lacking (Maan and Seehausen, 2011; Smadja and Butlin, 2011). In the empirical literature, observation of divergent mate preferences for ecologically relevant traits, likely to be widespread, is sometimes interpreted as evidence for magic trait speciation. However, such preferences may be the result of many generations of indirect selection. Experimental genetic or population genomic work would be required to distinguish the alternatives.

Conclusion

We suggest that magic traits that pleiotropically affect mating preferences, rather than mating cues, should be considerably more powerful in causing reproductive isolation than the reverse. This prediction may be tested in theoretical models that quantify the extent of reproductive isolation that is achieved by divergent selection on mating preferences vs. mating cues. Ultimately, however, we need more data from natural systems. It is a general problem in behavioural and evolutionary ecology that variation in mating signals is much better studied than variation in mating preferences (Kirkpatrick and Ryan, 1991; Bakker and Pomiankowski, 1995; Jennions and Petrie, 1997; Chenoweth and McGuigan, 2010). We hope that the current interest in magic trait speciation will inspire as much research effort into magic preferences as it does into magic cues. This is required for a better understanding of the distinct but intricately linked effects of sexual and natural selection in speciation.

Acknowledgements

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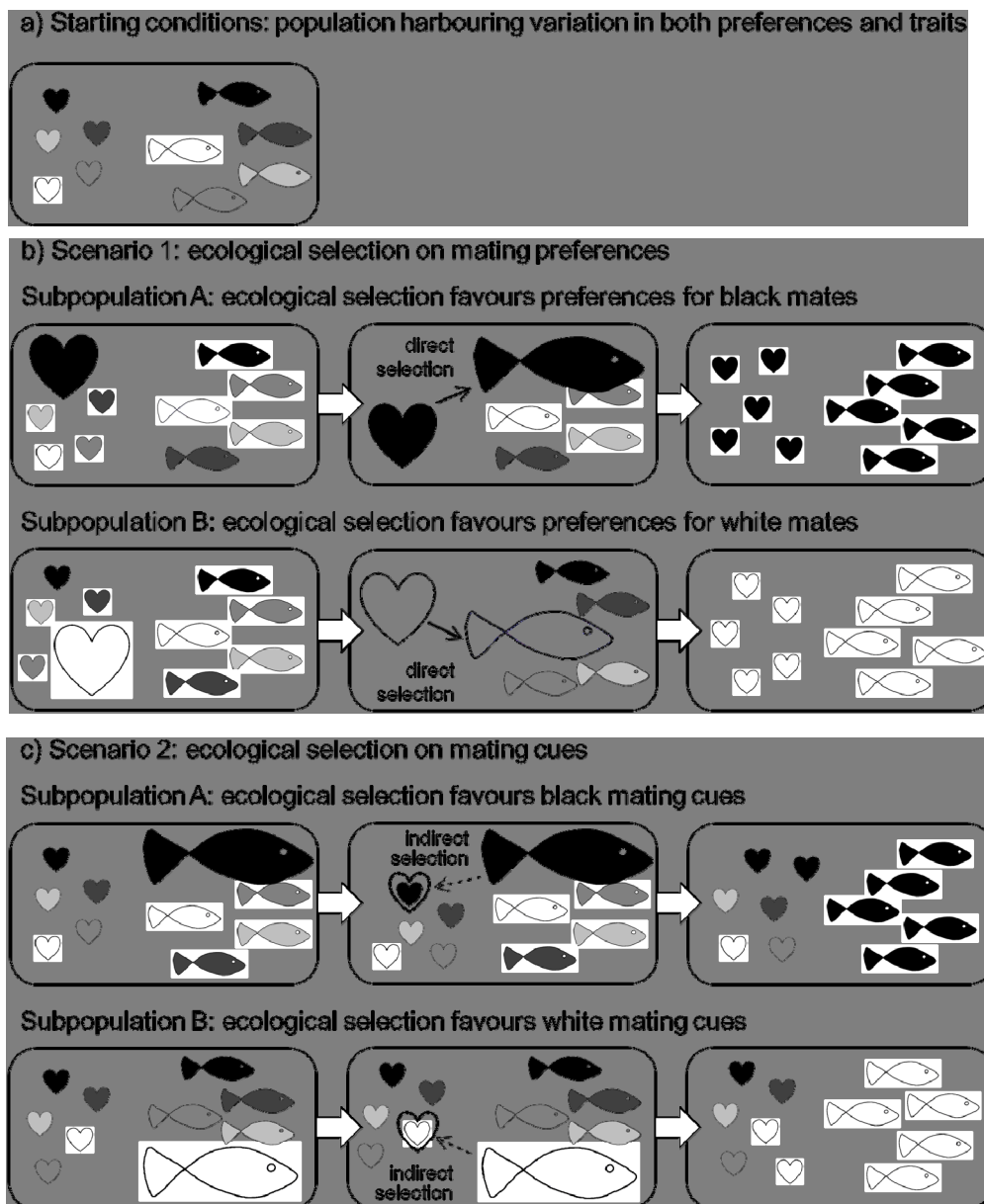
Figure 1. Effects of ecological selection on mating preferences and mating cues. a) Starting conditions: a population harbouring genetic variation for both preferences and cues. b) Evolutionary scenario in which mating preferences are subject to ecological selection, but mating cues are not. Divergent selection drives alternative mating preferences to fixation in two subpopulations. These preferences subsequently exert direct selection on mating cues, ultimately resulting in the fixation of alternative mating cues in each subpopulation. In this scenario, subpopulations will fix alternative preferences and cues and become reproductively isolated by mate choice. c) Evolutionary scenario in which mating cues are subject to ecological selection, but mating preferences are not. Divergent selection increases the frequencies of alternative mating cues in two subpopulations. This induces indirect selection on mating preferences, up to the point that a single mating cue becomes fixed in each subpopulation. Once there is no more variation in mating cues, selection on mating preferences is eliminated. At equilibrium the subpopulations continue to harbour variation for mating preference despite the fixation of a single mating cue in each one. They do not achieve reproductive isolation by mate choice.