Pleiotropy, “sexy” traits, and speciation

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The evolution of mating signals and preferences assists speciation by facilitating assortative mating within diverging lineages, thereby closing down conduits of gene flow between lineages. However, sexual communication traits are frequently subject to stabilizing selection, suggesting that new variants will be selected against, thereby discouraging their divergent evolution. Pleiotropic mutations may assist the evolution of sexual communication systems by introducing genetic covariation to signal and preference traits. New data from a range of taxa and sensory modalities are challenging more traditional views on the general importance of pleiotropy in sexual signaling systems. Key words: mate recognition, pleiotropy, sexual selection, speciation

PLEIOTROPY AND SEXUAL COMMUNICATION

Sexual communication traits are often distinctive between sister species and, correspondingly, play a role in sexual isolation. Components of sexual communication frequently experience stabilizing selection within species (e.g., Brooks et al. 2005) due to the expression of unimodal preference functions, wherein extreme signal values are less attractive, which may facilitate assortative mating and thus contribute to reproductive boundaries between diverging species. However, such selection against novel variants should reduce the potential for evolutionary divergence of these traits, suggesting a conundrum: how do such coordinated systems diversify in the face of stabilizing selection? One idea is that mutations with pleiotropic effects on both signals and preferences depress the effect of stabilizing selection because signal variants enter the population “coupled” to preference variants (Butlin and Ritchie 1989). Pleiotropic mutations simultaneously add genetic variation to signal and preference as well as establish positive genetic correlations required for the action of several powerful mechanisms of sexual selection and rapid speciation. These features should both mitigate the homogenizing effects of stabilizing selection and elevate the chance of fixation over nonpleiotropic mutations. In addition, the lack of recombination between signal and preference variants could buffer differentiated mate recognition systems from the degrading effects of hybridization during periods of secondary contact, assisting the process of reinforcement. Despite a long history to this hypothesis (Alexander 1962; Butlin and Ritchie 1989; Boake 1991), pleiotropy underlying sexual communication has been difficult to examine empirically and considered unlikely theoretically; consequently, pleiotropy is rarely considered in sexual selection models (Gavrilets 2004). However, modern genetic tools are now providing insights into the genetic architecture of sexual preference systems, yielding several potential cases of pleiotropy from a range of taxa and sensory modalities that challenge more traditional views on the generality of pleiotropy in sexual signaling systems. Here, we discuss 4 such examples, the first 2 from mutational studies in model organisms and the latter 2 from genetic studies of variation in natural systems

CHEMICAL COMMUNICATION IN DROSOPHILA

A study involving chemical signaling in Drosophila melanogaster provided the first illustration of a single gene having a pleiotropic effect on both a signal and its recognition. In Drosophila, suites of cuticular hydrocarbons (CHCs), expressed by both males and females, act as short-range or contact pheromones in sexual discrimination and sexual isolation between species (Ferveur and Sureau 1996; Billeter et al. 2009). The composition of CHCs depends on many genes, one of which is desat 1 (Coyne et al. 1999). In a recent study, Marcillac et al. (2005) examined the effects of a desat 1 transposable element insertion on the expression of CHCs and the ability of males to discriminate between the sexes. Lines that possessed the transposon had lower CHC abundance (causing smaller sex differences) than both the ancestral control line and a descendant line from which the transposon had been excised. Moreover, mutant males showed poorer discrimination between control males and females implying that the mutation changed not only the sexual signal but also its recognition. Expression of desat 1 in a chemosensory hair (Marcillac et al. 2005) suggests its involvement in sex pheromone perception, perhaps by altering the activity of genes coding enzymes involved in pheromone degradation.

VISUAL COMMUNICATION IN MEDAKA

Japanese medaka, Oryzias latipes, provide another example of pleiotropically controlled components of sexual communication. This fish species is variable for skin color and exhibits both female and male mate choice. A single 11-bp deletion in the somatotelin alpha (SLα) gene reduces xanthophore pigment cell size and abundance such that mutant lines appear gray in comparison with the brown wild-type (Fukamachi et al. 2004). Fukamachi et al. (2009) examined mutational effects of SLα on male mate choice in wild-type, mutation line, and transgenic medaka and showed that wild-type males discriminate against SLα mutant females using visual cues from xanthophores. In contrast, SLα mutant males occasionally preferred similarly colored SLα mutant females. In striking fashion, the authors also demonstrated strong assortative mating within both the SLα deletion line and a novel transgenic line overexpressing SLα, providing further evidence of a role for SLα influencing male mate choice. Although Fukamachi et al. (2009) focus primarily on male mate choice, SLα-mediated female mate choice might also exist, as the authors also

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found that females required significantly more solicitations by SlLa mutant compared with wild-type males prior to spawning.

**VISUAL COMMUNICATION IN Heliconius BUTTERFLIES**

The mutational studies discussed above indicate a pleiotropic link between signal and preference, but whether the genes responsible underlie natural variation in signal and preference is unknown. Two recent studies provide genetic association data consistent with pleiotropy in nature. The first comes from the butterfly genus *Heliconius* in which colorful wing patterns are well-known aposematic signals that also function in mate male preference and assortative mating (Jiggins et al. 2001). Kronforst et al. (2006) tested for a genetic association between mate preference and color pattern in the closely related *H. cydno galanthus* and *H. pachinus*. The authors found pronounced male preference for conspecific female wing patterns, with *H. cydno* males preferring white and *H. pachinus* preferring yellow, wing patches—segregating color traits governed by a single autosomal locus (Naisbit et al. 2003). Biometrical analysis suggests a simple genetic basis to male mate preference, which in turn significantly associates with wing color, in F2 hybrid progeny. Quantitative trait locus (QTL) mapping revealed perfect linkage between wing color, male mate preference, and allelic variation in wingless (wg), an autosomal locus previously implicated in lepidopteran wing patterning. Taken together, these results provide a compelling case for a tight genetic link between mate preference and signal.

**ACOUSTIC COMMUNICATION IN Laupala CRICKETS**

Although the 3 examples above demonstrate a genetic association between “male” preference and “female” signal, one additional system is consistent with pleiotropic control of female preferences for male signals. As in most crickets, males in the Hawaiian genus *Laupala* express sex-limited singing behavior in courtship that attracts females (Shaw and Herlihy 2000). Temporal song patterns of sympatric, as well as closely related allopatric, species are distinctive in *Laupala*, and females prefer the temporal patterns of conspecific males (Mendelson and Shaw 2002). In a recent study, segregation in F2 hybrids between closely related *L. kohalensis* and *L. paranigra* revealed a genetic association between QTL for male song rate and female acoustic preference (Shaw and Lesnick 2009). Further investigation of backcross introgression lines isolating song QTL alleles from the slow-singing species (*L. paranigra*) in the fast species (*L. kohalensis*) background revealed colocalization between song and preference on a second autosomal linkage group and a genetic correlation indicative of genome-wide physical associations between these 2 traits (Wiley and Shaw 2010).

**CONCLUSION**

Genetic correlations can play a profound role in the evolution of complex traits, and pleiotropy provides a potent mechanism to produce such correlations. For example, it has long been recognized that traits under disruptive selection due to ecological advantages in different habitats could trigger speciation if they simultaneously caused assortative mating by habitat (essentially, through pleiotropy), thereby curtailing gene flow between habitats. Sexual communication traits could represent a compelling counterpart to such “magic traits” (Gavrilets 2004) if signal and preference components are under pleiotropic control (i.e., “sexy traits” which we define as sexual communication traits with pleiotropic effects on both signal and preference). One of the advantages to making such observations in model organisms is the potential for identifying genetic, biochemical, and developmental mechanisms underlying the pleiotropic effects. Natural systems, on the other hand, offer an evolutionary context for interpreting the consequences of pleiotropy in sexual communication, although it is often difficult to distinguish tight physical linkage from pleiotropic effects of signal and preference loci (as is currently the case in *Heliconius* and *Laupala*). Advances in genetic mapping and gene discovery techniques are enabling more penetrating analyses of such nonmodel organisms, however. Growing literature in both types of systems bolsters the importance of this exciting possibility.

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