

COMMENTARY

Individual mating decisions and hybridization

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The dynamics of gene flow among populations ultimately depend on behavioural interactions among individuals (Ritchie, 2007), construed in the broadest sense to encompass chemical and mechanical interactions in plants and microorganisms. The mechanisms underlying mate choice can, therefore, determine whether hybridization promotes or retards speciation. Further, the nature of the processes underlying mating decisions imposes important constraints on their role as agents of selection. Understanding the evolutionary genetics of hybridization requires a more detailed consideration of what determines mating interactions among individuals. For hybridization to have notable evolutionary consequences, two things have to happen: first, matings have to occur between males and females from divergent populations and second, hybrids have to mate with each other and/or backcross to parentals. There is a growing body of evidence to suggest that behavioural barriers to interspecific mating are brittle and susceptible to environmental perturbation. Once hybridization occurs, novel suites of signals and novel suites of preferences can facilitate backcrossing to parentals or, alternatively, can lead to hybrid speciation. I will discuss each of these processes in turn.

Individual decisions and interspecific matings

Signal detection theory and interspecific matings

Mate choice is a continuum spanning species boundaries. While choosers may evaluate different signals when attending to inter- or intraspecific signal variation, conspecific mate recognition and within-species mate choice ultimately represent a unitary process from an individual's point of view (Ryan & Rand, 1993). Signal detection theory provides a useful framework for thinking about mating decisions (Wiley, 2006). A chooser can either accept or reject a potential mate (coercive matings will be discussed later). Assuming a fitness cost to hybridization, choosers are faced with an unavoid-

able trade-off: be permissive and accept a broad range of mates, and risk incurring higher fitness costs due to hybridization; or be picky and accept a narrow range of mates, and risk reduced fitness due to costs of choice or missed mating opportunities. In general, if species are closely related enough to permit interspecific gene flow, there is likely to be some overlap in the way that mating signals are perceived by choosers. Under a wide variety of circumstances, choosers will exhibit some degree of permissiveness and therefore accept heterospecific matings.

Ecological conditions affect mating decisions

It has long been recognized that hybridization is particularly common in disturbed and edge habitats (Mayr, 1942; Anderson, 1948). There are at least three ways that this phenomenon can be explained in terms of individual mating decisions. The first is that environmental disturbance can impair sexual communication such that it is impossible for choosers to discriminate conspecifics from heterospecifics. For example, eutrophication caused by increased nutrient load acts to restrict transmission or reception of both visual and olfactory signals, which has resulted in hybridization in two groups of freshwater fishes (reviewed in Rosenthal & Stuart-Fox 2012). While most studies have focused on anthropogenic impacts, natural events can also produce phenomena like eutrophication. Disturbance episodes may therefore play an important role in driving hybridization between lineages.

Second, multiple ecological processes can alter search costs for choosers. If conspecific mates are rare (Willis *et al.*, 2011) or if predators make it risky to search for conspecifics (Willis *et al.*, 2012) choosers may opt to mate with heterospecifics. Ecological variation may also drive the fitness of hybrid offspring themselves. Female spadefoot toads mate preferentially with heterospecifics under conditions where water is scarce, when hybrids gain a fitness advantage from maturing early (Pfennig, 2007). In all of these cases, there may be a net benefit to mating with heterospecifics even if hybrids have lower average fitness than parentals.

Third, there is increasing recognition that learning plays a ubiquitous role in the development of mating preferences (reviewed in Verzijden *et al.* 2012). If unrelated conspecifics are rare, choosers may develop preferences for familiar heterospecific phenotypes or antipathy towards familiar conspecifics.

These properties of mate choice all suggest a major role for a broad range of abiotic, community-ecological and social inputs in determining whether hybridization occurs. Thus, ecological conditions can have a dispositional influence on whether reproductive isolation will be enhanced or destroyed when incompletely isolated populations come into contact. All of these factors can act together to promote hybridization as a consequence of

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environmental change via effects on mate-choice mechanisms. Given that hybrids are fertile, ecological circumstances may play a greater role in determining the evolutionary fate of hybrids than any genetic differences between hybridizing populations.

Individuals vary in their propensity to hybridize

Within a hybridizing system, some individuals are more likely than others to engage in interspecific matings. The major source of variation is sex. Discrimination against heterospecifics is usually much stronger in females. Males generally have little to gain and much to lose by passing up a mating, and it is not atypical for males to mate with inanimate objects. Even if males reap zero direct fitness benefit from mating with a heterospecific female, they may increase their probability of mating with conspecifics via mate-choice copying (Schlupp *et al.*, 1994). Further, males frequently subvert conspecific preferences through forced mating, resulting in hybridization (the so-called satyr effect (Gröning & Hochkirch, 2008)). Thus, hybridization can occur as a result of male behaviour even in the face of very strong conspecific preferences in females.

The evolutionary history of the two hybridizing species also influences the propensity to hybridize. Asymmetric hybridization, whereby females of one species are more likely to mate with males of the other than the reverse, appears to be quite common (Wirtz, 1999). Asymmetric hybridization can arise from males of one species being more successful at coercive mating (Gröning & Hochkirch, 2008), but it can also arise from individuals of one species being globally more attractive to choosers (Stein & Uy, 2006). In either case, asymmetric hybridization represents a potentially very interesting case of asymmetric fitness of parental genotypes, because loci associated with mate choice are often sex-linked. The form of sex linkage can have a determining effect on the elaboration of traits and preferences (Kirkpatrick & Hall, 2004), and epistatic interactions involving sex chromosomes can be key drivers of reproductive isolation (Presgraves, 2008). The interaction between sex linkage and asymmetric hybridization represents a potentially fruitful area of evolutionary-genetic research.

Finally, within one sex of one species, some individuals might be more prone to hybridizing than others. For example, males with particular trait values might be more attractive to heterospecific females than others; on the other hand, some choosers may be more attracted to heterospecific traits or less discriminating (Jennions & Petrie, 1997). In a species of swordtail fish, females that prefer large body size are less likely to discriminate against heterospecifics (Rosenthal & Ryan, 2011). In addition, choosers are likely to vary in how they respond to the environmental factors described previously.

Heritable variation in the propensity to hybridize has important evolutionary consequences. As Abbott *et al.* (2013) point out, 'selection against mating with heterospecifics will inevitably result in novel patterns of selection on conspecific choosers'. Similarly, interspecific matings by a nonrandom subset of individuals will influence the evolutionary trajectory of hybrid lineages.

Given the fragility of behavioural isolating mechanisms and the likelihood that at least some individuals within a population will be likely to mate with heterospecifics, it is not at all surprising that we find hybrids under every bush. Yet, the evolutionary consequences of hybridization depend on the fitness of hybrids, which in turn depends on mate choice by and for hybrids. What might the hybrids be up to under those bushes?

Mating decisions and hybrid phenotypes

Hybridization produces novel mating phenotypes

All of the points about interspecific matings in the preceding section apply just as well to matings between parentals and hybrids. Crucially, however, recombination, transgressive segregation and complex epistatic interactions can produce both novel display traits and novel mating preferences, which can have potentially dramatic effects on evolutionary trajectories. In some cases, these phenotypes may be globally disadvantageous, in which case they merely represent a special case of hybrid unfitness. In other cases, however, they may favour hybrids backcrossing to one or both parent species or to each other.

Novel and exaggerated display traits may be more attractive to choosers

Abbott *et al.* (2013) outline the major genetic mechanisms involved in generating phenotypic diversity among hybrids. Each of these is expected to have a major impact on both mating signals and mating preferences.

By extending the range of phenotypic variation, transgressive segregation could result in sexual display traits that are more elaborate in some hybrids than in parental species. Many mating preferences are directional, with choosers preferring whichever trait confers greater sensory stimulation (Ryan & Keddy-Hector, 1992). Higher mating success due to increased attractiveness could more than compensate for a viability cost of hybridization (Brooks, 2000).

In addition to exaggerating (or diminishing) single traits, hybridization can also produce novel multivariate phenotypes through recombination or through novel epistatic interactions. Multivariate mate choice is the norm, and both mechanistic constraints and the depletion of genetic variance by sexual selection make it likely that choosers are most attracted to combinations of traits that are effectively unavailable in nature (Van

Homrigh *et al.*, 2007; Fisher *et al.*, 2009). By relaxing phenotypic correlations, hybridization again has the potential to produce globally more attractive males. Thus, even if interspecific matings between parent species are rare, and even in the face of natural selection against hybrids, the attractiveness of hybrid signals could provide a conduit for genetic exchange between species.

Hybrid choosers exhibit novel mating preferences

The same rules that govern the effects of hybridization on display traits also apply to the mechanisms used by choosers to sense, perceive and evaluate those traits. Sensory receptor genes, for example, are not exempt from transcriptome-wide patterns of mis-expression in hybrids. Reduced expression of receptor genes could have an effect similar to that of environmental disturbance of sensory channels, resulting in permissive mate choice and indiscriminate mating by hybrid choosers. Alternatively, hybrids may backcross preferentially to one or the other parent species. Hybridization could also result in novel preferences for individual traits or trait combinations, such that hybrid choosers favour different trait values than do parentals. These novel preferences thus have the potential to act as agents of sexual selection that drive both hybrid and parental phenotypes in unexpected directions.

The hierarchical nature of multivariate mating preferences also has the potential to influence patterns of introgression across hybrid zones. From a chooser's point of view, not all display traits are created equal. One trait, like a particular acoustic feature or odourant molecule, may be required to elicit conspecific mate recognition. Additional traits may enhance attractiveness, but choosers will fail to respond unless the appropriate recognition cue is present. For example, in swordtail fish, species-typical preferences for pheromones override asymmetric preferences for visual cues: females will reject a male producing heterospecific pheromone even if he bears an attractive visual signal (Hankison & Morris, 2003).

In this scenario, genetic differences between species in their response to recognition cues would correspond to Abbott *et al.*'s (2013) 'barrier loci' with epistatic effects on overall preferences. Later-generation hybrids could thus backcross preferentially to one or the other parental species depending on their own genotype. This pattern could prevent rampant hybridization while nevertheless serving as a conduit for interspecific exchange of alleles for preferences associated with other display traits, changing the mating preferences of hybridizing populations relative to allopatric populations.

Traits, preferences and the evolutionary consequences of hybridization

Hybridization's effects on trait and preference mechanisms ultimately mean that backcrossing may be more

frequent than expected and that enhanced attractiveness may have a compensatory effect on the fitness of hybrid males. Depending on spatial and temporal patterns of selection on hybrids and on the nature of hybrid preferences, the outcome may be introgression into parental lineages or hybrid panmixia. At the same time, effects on traits and preferences make it extremely unlikely that hybrid display traits will be genetically coupled to hybrid preferences in early-generation hybrids unless trait-preference combinations are one-dimensional and associated with closely linked genetic loci (Shaw & Lesnick, 2009). Individual hybrids will be attractive to, and attracted by, individuals from one or both of the parental species. Accordingly, homoploid hybrid speciation alongside coexisting parental species should be rare in the absence of ecological differentiation.

Conclusions and next steps

We are beginning to gain a good understanding of the proximate factors that lead individuals from divergent populations to mate and produce first-generation hybrids. Behavioural isolating mechanisms are not robust, and the production of first-generation hybrids by closely related, sympatric individuals should be a frequent occurrence. A handful of studies have shown that first-generation hybrids show intermediate traits and preferences relative to parentals (Hoy *et al.*, 1977; Doherty & Gerhardt, 1983), which should encourage hybrid-hybrid matings.

Phenotypic and transcriptomic studies of hybrids predict that later-generation hybrids should show novel and transgressive combinations of both traits and preferences. Later-generation hybrids in the wild show transgressive combinations of traits (Culumber *et al.*, 2011) but we know very little about how preferences are expressed in natural or artificial hybrids beyond the first generation.

As suggested by Abbott *et al.* (2013), knowing the genes associated with variation in mating traits would be invaluable to our understanding of hybridization and speciation. Integrative studies have the potential to shed light both on the genetic mechanisms underlying hybrid traits and preferences and on their evolutionary consequences, in a three-step process. First, behavioural experiments and multivariate studies of mating patterns on both parentals and hybrids can be used to characterize how choosers evaluate suites of mating signals, thereby generating prediction about how traits and preferences should move across natural hybrid zones. Second, quantitative trait locus (QTL) mapping of multivariate traits and preferences can be used to identify elements of the genetic architecture associated with interspecific differences in mating traits. Third, the distribution of these QTL both across contemporary natural hybrid zones and along phylogenies of closely related species can be used to test predictions about

how mating traits should interact to influence genetic exchange across hybrid zones.

Such an approach has the potential to greatly advance our understanding of the evolutionary genetics of the display traits that are the target of mate choice, particularly in light of recent advances in comparative genomics. Understanding the other side of the equation—preferences—is rather more problematic, as we are only beginning to understand the genotype by environment interactions that determine preference expression. A more sophisticated picture of the mechanistic underpinnings of mating preferences will enhance our ability to grasp their central and unusual influence on genetic exchange among populations.

Acknowledgments

I thank Rongfeng Cui, Hanna Kokko, and an anonymous reviewer for their helpful comments on drafts of this manuscript.

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Received 14 August 2012; revised 28 August 2012; accepted 1 September 2012