

IDEA AND PERSPECTIVE

Speciation via species interactions: the divergence of mating traits within species

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Abstract

A species may overlap with a mosaic of species across its geographic range. Many types of species interaction cause selection on mating traits, but their role in generating within-species divergence has been neglected. The pattern of reproductive character displacement (RCD) has been classically attributed to reinforcement, a process driven by selection against hybridisation. Recent reinforcement research shows that sexual isolation can result between displaced and non-displaced populations. We argue that RCD (and hence potentially speciation) among populations can be generated by a variety of fundamental species interactions beyond reinforcement. We unify these interactions under one process of mating trait divergence and speciation ('RCD speciation'). This process can occur in many geographic settings. Because selection is acting directly on mating traits, rapid speciation can result involving little differentiation in other traits. This pattern of diversification is seen in many groups and regions, and has previously been attributed to sexual selection alone.

Keywords

Community ecology, disruptive selection, ecological speciation, mating preferences, mating signals, magic traits, reinforcement, reproductive character displacement, sexual selection, sympatric speciation.

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INTRODUCTION

How new species arise from an existing species remains a fundamental question in evolutionary biology. Particularly intriguing is the widely-observed pattern noted by Darwin (1859) that related species, in some cases highly speciose groups, often differ primarily (and often almost solely) in mating signals. This pattern suggests that one of the most important forms of reproductive isolation in animals is differences in mate choice among populations (called 'sexual isolation', Mayr 1963; Ritchie 2007). This view is supported by a meta-analysis revealing that selection on traits involved in mating is on average two times stronger than selection acting on traits that influence survival or fecundity (Kingsolver & Pfennig 2007). Mate choice underlying sexual isolation depends on mating signals and associated preferences for those signals (here referred to together as 'mating traits'), and any divergence of mating traits among populations may initiate sexual isolation and speciation (Endler 1989; Andersson 1994; Coyne & Orr 2004). Understanding the processes that generate mating trait divergence among populations lies at the core of speciation research.

The pattern of divergence primarily in mating traits (generally involving marked sexual dimorphism) has been interpreted as evidence for the causal action of sexual selection as a driver of speciation (West-Eberhard 1983; Price 1998; Shuster & Wade 2003; Coyne & Orr 2004; Ritchie 2007). Indirect support for this hypothesis has been provided by comparative analyses of various taxonomic groups that have found that signatures of sexual selection are correlated with increased speciosity (reviewed in Panhuis *et al.* 2001; Coyne & Orr 2004; Ritchie 2007). Also supporting this hypothesis, theoretical modelling has shown that differences in mating signals and preferences among populations may be initiated by random outcomes of the sexual selection process itself (such as drift: Lande 1981; Kirkpatrick & Ryan 1991; and mutation: Nei *et al.* 1983; Wu 1985). The strongest empirical evidence for the role of sexual selection in speciation comes from the effect of the physical signalling environment (sensory drive: Endler 1992; Boughman 2002) and conflict between the sexes (sexual conflict: Parker & Partridge 1998; Gavrillets & Hayashi 2005; Hosken *et al.* 2009). However, convincing examples are sparse and it remains to be conclusively shown that sexual

selection is a major driver of this pattern (Schluter 2001; Andersson & Simmons 2006; Ritchie 2007). This has led to the suggestion that sexual selection's role in speciation is most likely in association with ecological selection or selection for species recognition (Ritchie 2007).

There is little doubt that the pattern of mating signal divergence does indicate that selection on mating signals and associated preferences plays an important role in speciation. Sexual selection is always operating on mating traits, but yet to be established is the relative importance of sexual selection vs. other selective processes in initiating and exaggerating mating trait divergence. One powerful source of selection that can generate divergence in mating traits among populations has been largely overlooked – the role of species interactions.

A form of species interaction based on mating traits is reinforcement between overlapping taxa. Reinforcement is the evolution of mating signals and preferences that increase sexual isolation in areas of overlap between taxa due to selection against hybridisation or attempted hybridisation (Dobzhansky 1951; Howard 1993; Servedio & Noor 2003). This process gives rise to a pattern of reproductive character displacement (RCD), classically defined as 'greater divergence of an isolating [mating] trait in areas of sympatry between closely related taxa [species or lineages] than in areas of allopatry' (Howard 1993), resulting in displaced and non-displaced populations that differ in mating traits. Alternatively, Butlin (1987) defined RCD and reinforcement as two processes of premating divergence – RCD for situations where hybrids have zero fitness (i.e. taxa are already 'good' species), and reinforcement for situations where hybrids have reduced (but not zero) fitness (i.e. involving gene flow between taxa). We follow the definition of RCD as a pattern of displacement in mating traits, along the lines of that defined by Howard (1993) above and as originally described by Brown & Wilson (1956).

The process of reinforcement is now well accepted due to convincing empirical examples (e.g. Noor 1995; Sætre *et al.* 1997; Rundle & Schluter 1998; Higgie *et al.* 2000; Nosil *et al.* 2003; Hoskin *et al.* 2005), and there are a number of comprehensive reviews (e.g. Howard 1993; Noor 1999; Servedio & Noor 2003; Rundle & Nosil 2005). Here we are not so much interested in the process of reinforcement itself, but rather the potential for incidental speciation between the resulting displaced and non-displaced populations – that is, speciation due to RCD. Recent research in systems where reinforcement is operating has shown that RCD can incidentally generate sexual isolation (Nosil *et al.* 2003; Higgie & Blows 2007, 2008) and lead to speciation (Hoskin *et al.* 2005) in this manner.

An important extrapolation is that many fundamental species interactions beyond reinforcement can also cause direct selection on mating traits, including predation, parasitoidism, pollination, mimicry, and competition for

signal space. Given that any one species can overlap with a mosaic of different species over its geographic range, such species interactions can potentially drive divergence in mating traits among populations, generating a pattern of RCD equivalent to that produced by reinforcement. In turn this may lead to speciation between displaced and non-displaced populations, as demonstrated in the reinforcement research. This kind of selection will generate a pattern of divergence in mating signals, and potentially speciation among populations, with little divergence in other ecological traits. Speciation through adaptation to the biotic landscape has been incorporated under the idea of 'magic traits' (see Box 1), but we extend this beyond the generally envisaged idea of mating trait change due to underlying selection for

Box 1 Magic traits

Local adaptation of populations to different biotic or abiotic environments has long been recognized as an important mechanism of speciation (Doebeli & Dieckmann 2000; Schluter 2001; Gavrilets 2004; Rundle & Nosil 2005). For adaptation to result in sexual isolation between populations, a genetic association is required between the ecological trait under disruptive selection and the mating trait, particularly under sympatric and parapatric settings (Maynard Smith 1966; Schluter 2001; Coyne & Orr 2004; Gavrilets 2004; Rundle & Nosil 2005). One way to achieve this is if the trait under disruptive selection is also the mating trait, termed 'magic traits' (Gavrilets 2004). The importance of such traits as a direct and potentially rapid mechanism of speciation has been long recognized (Maynard Smith 1966) and they form the basis of many sympatric speciation models (reviewed in Gavrilets 2004).

Under a broad definition of magic traits – any trait simultaneously involved in local adaptation and mate choice (Gavrilets 2004) – disruptive selection can either act on a trait that functions (i) both in ecology and mating or (ii) purely as a mating trait. The first is the most commonly envisaged, for example, changes in colour pattern due to mimicry (Jiggins *et al.* 2001), or body size (Nagel & Schluter 1998) or beak shape (Podos 2001) due to divergence in feeding ecology, simultaneously affect mating behaviour. In the second, such traits are not particularly 'magic' because disruptive selection is acting directly on them in their sole role as mating traits and not via a simultaneous ecological function. Both are covered here because, viewed in either sense, the species interactions cause direct selection on the mating trait.

an ecological function (e.g., mimicry), to interactions causing direct evolution of mating traits. We believe the scope and importance of these species interactions as a speciation mechanism have been largely overlooked.

Here we review the reinforcement literature showing that RCD can incidentally drive sexual isolation. We then extend the scope of RCD to incorporate the numerous fundamental species interactions that can also generate this pattern, unifying them under one process of mating trait divergence that can result in speciation. We outline how this could be a significant process of diversification in many settings, and may be responsible, at least in part, for the intriguing pattern of related species (including some diverse radiations) that differ in little other than mating signals.

SECONDARY EFFECTS OF RCD BY REINFORCEMENT

Rather than reviewing reinforcement, our interest here is to outline the degree to which reinforcement with another taxa can incidentally drive mating trait divergence among populations – that is, the potential for speciation between displaced and non-displaced populations within a species. When a species uses a single mechanism for both species recognition and sexual selection (e.g. frog call), reinforcing selection may affect the way sexual selection operates within a species. This is because in populations of a species that do not co-exist with a closely-related taxon (i.e. allopatric populations), sexual selection operates on mating signals and preferences without the constraint of reinforcement (e.g.

Pfennig 2000; Higgie & Blows 2007, 2008). In sympatric populations, however, the presence of reinforcing selection on the same traits increases the complexity of the mate choice process because now individuals must also choose the correct lineage to avoid costs associated with hybridisation or attempted hybridisation. This may cause differences in signals and preferences between reinforced (sympatric) and non-reinforced (allopatric) populations, hence potentially resulting in sexual isolation and speciation between them (Littlejohn & Loftus-Hills 1968; Zouros & d'Entremont 1980; Howard 1993; Schluter 2001; Nosil *et al.* 2003; Hoskin *et al.* 2005; Pfennig & Ryan 2006; McPeck & Gavrilets 2006; Higgie & Blows 2007, 2008) (Fig. 1).

In two overlapping Australian *Drosophila* species, reinforcing selection caused populations of *D. serrata* sympatric with *D. birchii* to diverge from allopatric populations (Higgie *et al.* 2000), whereas sexual selection favoured and maintained the non-reinforced allopatric phenotype (Higgie & Blows 2008). These two selective processes thereby prevented the merging of the sympatric and allopatric phenotypes of *D. serrata* where they meet, resulting in divergent mating signals and preferences in parapatric populations (Higgie & Blows 2007). Similarly, reinforcement in parapatric populations of *Timema cristanae* walking-stick insect ecotypes has also resulted in females from reinforced populations showing increased mating discrimination relative to allopatric populations (Nosil *et al.* 2003). In the green-eyed treefrog (*Litoria genimaculata*) reinforcement between two genetic lineages has resulted in an allopatric speciation event between a population that has been reinforced

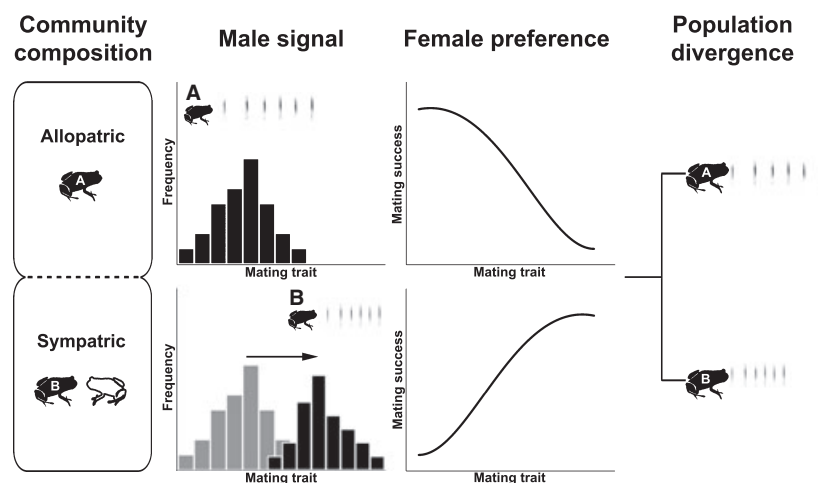


Figure 1 Speciation resulting from reproductive character displacement. Schematic of how species interactions in different populations can drive divergence in mating traits, resulting in speciation. The focal species (black frog) can overlap with different species over its geographic range. Here we show population A is allopatric, while population B is sympatric with a different species (white frog). Population A and B may be allopatric or parapatric to each other (dotted line). Direct selection on mating traits caused by the different species interactions results in reproductive character displacement in signal and/or preference. The resulting divergence in mating traits may be large enough to cause the black frogs to mate assortatively among populations, and diverge into two species. An alternative scenario is that each population is sympatric with a different species.

and populations that have not (Hoskin *et al.* 2005; Hoskin 2007).

Reinforcement has previously been dismissed as a potential cause of the pattern of divergence in mating traits as it could not account for allopatric speciation (Ritchie 2007). However, reinforcement can have a two-fold role in causing speciation: the traditional, direct role where selection against hybridisation results in speciation of sympatric populations (e.g. Sætre *et al.* 1997; Hoskin *et al.* 2005); and in this indirect role, where allopatric or parapatric speciation can result as a byproduct of reinforcing selection (e.g. Hoskin *et al.* 2005). Therefore reinforcement can also cause the pattern of divergence in mating traits.

OTHER SPECIES INTERACTIONS THAT CAN GENERATE RCD

In addition to reinforcement imposed by selection against attempting to mate with a closely related species, there are a suite of species interactions that may also directly affect a species' mating traits. Any species interaction that is carried out on the basis of traits involved in mating, where there is a cost or benefit to the interaction for either party, can also exert selection on those same traits. Here we expand the definition of RCD to be a pattern generated by any species interaction that displaces mating traits. This expanded definition reframes RCD as a pattern caused by many processes of species interaction, more clearly separating pattern from process by removing the unnecessarily dependent relationship between RCD and reinforcement. This expanded definition of RCD does not require the interacting species to be closely related (i.e. hybridizing or attempting to hybridize), as is required in the 'classic' definition of RCD caused by reinforcement (Brown & Wilson 1956; Howard 1993; Servadio & Noor 2003).

Here we provide examples from species interactions involving predation and parasitoidism, pollination, brood parasitism, mimicry, and competition for signal space. The key point is that all these examples involve species interactions based directly on mating traits, and this may vary geographically. This is not an exhaustive list, rather we present representative examples from a range of fundamental species interactions (summarized in Table 1).

Predation and parasitoidism

The most obvious examples are where the focal species (whose mating traits we are interested in) is preyed upon by a predator or parasitoid that exploits their visual, audio or chemical mating signals and preferences (reviewed in Zuk & Kolluru 1998; Haynes & Yeorgan 1999). Species are generally most conspicuous when they are signalling. Predators and parasitoids can locate their prey by either

eavesdropping on the signal (thus exerting selection on signal) or by mimicking the signal themselves (thus exerting selection on the preference) (Haynes & Yeorgan 1999). There is no reason to expect that predators or parasitoids occur over the full geographic range of their prey because although they are directly dependent on their prey, the converse is not true. Therefore there may be populations of the focal species that are sympatric and allopatric to their predator or parasitoid.

For example, across Australia and the Pacific, the males of field crickets (*Teleogryllus oceanicus*) attract females by singing. However, on a single island in Hawaii singing males are parasitized through eavesdropping by an acoustically-orientating fly, *Ormia ochracea*. Seemingly as a consequence of this selection, the males on this island have stopped singing over a period of less than 20 generations (Zuk *et al.* 2006). It has yet to be examined whether this change in sexual signalling of the parasitized population may result in sexual isolation from other unparasitized *T. oceanicus* populations.

Another example of parasitoidism, but through chemical signalling, is exploitation of the mating behaviour of a solitary bee (*Habropoda pallida*). Female bees of this species release pheromones for males to locate them to mate. Larvae of a parasitoid blister beetle (*Meloe franciscanus*) exploit this by forming aggregations that cooperatively release a chemical pheromone mimicking the pheromone of female bees, thus luring the male bee to them (Saul-Gershenz & Millar 2006). These larvae then climb on to the male's body, transfer to a female bee when the male bee finally finds a mate, then parasitize her eggs when she lays them (Saul-Gershenz & Millar 2006). Due to the cost of being parasitized there should be selection on male bees to improve their discrimination of female bees from larval blister beetle aggregations. There may also be selection on female bee signal to produce a blend of pheromones differing from that produced by the blister beetle aggregation, thus potentially avoiding mating with males that are attracted to the blister beetle pheromone and therefore carrying parasites. Males who have a preference for this alternative blend will leave more offspring than males lured to the blister beetle blend. Populations of the solitary bee also exist in allopatry without the blister beetle parasitoidism so there is a possibility in this system for parasitized (sympatric) and unparasitized (allopatric) populations of the solitary bee to diverge in mating traits.

Pollination

Pollination is another species interaction where mating traits can be exploited. Many orchid species are pollinated through sexual deception. For example, the orchid *Chiloglottis trapeziformis* produces chemicals that imitate the female pheromones of thynnine wasps (*Neozeleboria cryptoides*) and

Table 1 Species interactions that may cause direct selection on mating traits. Representative examples of each of these are given, including whether RCD in signal and/or preference have been demonstrated. This is not a comprehensive list – many other systems are amenable to testing this process

Interaction	Process (geographic variation due to...)	System	Mating Signal	RCD in Signal	RCD in Preference	Refs
Reinforcement	Selection against mating with closely related species/lineages/morphs	<i>Litoria genimaculata</i> lineages (frogs)	Mating call (♂)	Yes	Yes (♀)	(1,2)
		<i>Drosophila serrata</i> / <i>D. birchii</i> (flies)	Pheromones (♂ and ♀)	Yes	Yes (♀)	(3-5)
		<i>Timema cristinae</i> ecotypes (walking-stick insects)	Pheromones? (♂)	Unknown (but correlated with ecotype)	Yes (♀)	(6,7)
Predation/ Parasitoidism	Selection against being located by predator/parasitoid via mating signal or preference	<i>Teleogryllus oceanicus</i> (cricket)/ <i>Ormia ocracea</i> (fly)	Mating call (♂)	Yes	Unknown	(8)
		<i>Habropoda pallida</i> (bee)/ <i>Meleoe franciscanus</i> (beetle)	Pheromones (♀)	Unknown	Unknown	(9)
Pollination (deceptive)	Selection against mistakenly mating with a sexually-deceptive flower	<i>Neozeleboria cryptoides</i> (wasp)/ <i>Chiloglottis trapeziformis</i> (orchid)	Pheromones (♀)	Unknown	Unknown	(10)
Brood parasitism	Selection for incorporating signals of parasitized species into own signals	<i>Vidua camerunensis</i> / <i>Lagonosticta</i> spp. (finches)	Mating call (♂)	Yes	Yes (♀) and shift in ♂ response to call	(11-14)
Mimicry	Selection for mimicking signals of another species, which are also used as signals within own species	<i>Heliconius melpomene</i> / <i>H. erato</i> and <i>H. cydno</i> / <i>H. sapho</i> (butterflies)	Wing pattern (♀)	Yes	Yes (♂)	(15,16)
		<i>Dendrobates imitator</i> / <i>Dendrobates</i> spp. (frogs)	Morph colour? (♂)	Possibly (yes, if morph colour is signal)	Unknown	(17)
Competition (signal space)	Selection for reduced competition in signal space	<i>Allobates femoralis</i> / <i>Epipedobates trivittatus</i> (frogs)	Mating call (♂)	No	Unknown (but shift in ♂ response to call)	(18)

1. Hoskin C.J. *et al.* (2005). *Nature*, 437, 1353–1356; 2. Hoskin C.J. (2007). *Biol. J. Linn. Soc.*, 91, 549–563; 3. Higgie M. *et al.* (2000). *Science*, 290, 519–521; 4. Higgie M. & Blows M.W. (2007). *Am. Nat.*, 170, 409–420; 5. Higgie M. & Blows M.W. (2008). *Evolution*, 62, 1192–1203; 6. Nosil P. *et al.* (2003). *Proc. R. Soc. B*, 270, 1911–1918; 7. Nosil P. *et al.* (2007). *Genetica*, 129, 309–327; 8. Zuk M. *et al.* (2006). *Biology Letters*, 2, 521–524; 9. Saul-Gershenz L.S. & Millar J.G. (2006). *Proc. Natl. Acad. Sci. USA*, 103, 14039–14044; 10. Schiestl F.P. *et al.* (2003). *Science*, 302, 437–438; 11. Payne R.B. *et al.* (1998). *Anim. Behav.*, 55, 1537–1553; 12. Payne R.B. *et al.* (2000). *Anim. Behav.*, 59, 69–81; 13. Sorenson M.D. *et al.* (2003). *Nature*, 424, 928–931; 14. Balakrishnan C.N. & Sorenson M.D. (2006). *Behav. Ecol.*, 17, 473–478; 15. Jiggins C.D. *et al.* (2001). *Nature*, 411, 302–305; 16. Jiggins C.D. *et al.* (2004). *J. Evol. Biol.*, 17, 680–691; 17. Symula R. *et al.* (2001). *Proc. R. Soc. B*, 268, 2415–2421; 18. Amézquita A. *et al.* (2006). *Evolution*, 60, 1874–1887.

so attract the male wasps (Schiestl *et al.* 2003). In their attempt to ‘mate’ with the orchid the male wasps instead transfer pollen they are carrying from previous ‘mating’ interactions with other orchids. Although the deceived males do not pay outright with their life or their offsprings’ lives (as opposed to the parasitoidism outlined above), male

wasps have been shown to deposit sperm on the orchid (Gaskett *et al.* 2008), therefore wasting gametic resources that they may not be able to replace before finding a female wasp to mate with. Furthermore, male wasps may miss out on matings relative to other males that are not deceived. Additionally, because female wasps are flightless, they are

dependent on the males finding them and taking them to a food source, and may starve if they cannot attract a mate (Schiestl & Peakall 2005). Therefore, selection should act to change the female pheromones and male preferences to avoid the orchids' deception. Allopatric populations of these wasps not subject to sexual deception by the orchids will not have this selective pressure acting upon them and therefore the sympatric and allopatric populations of wasps may diverge in their mating traits.

Brood parasitism

Brood parasitism is a species interaction that may result in speciation of the parasites through mimicry of their hosts. Indigobirds (*Vidua* spp.) are brood parasites of a number of different species of estrildid finches across Africa. In a well-studied example, the Cameroon indigobird (*Vidua camerunensis*) parasitizes several host species of finch (*Lagonosticta* spp.) in West Africa but is called a single species because the host races are indistinguishable in morphology (Payne *et al.* 2005) and neutral genetic markers (Sefc *et al.* 2005). Male indigobirds imprint on their host race by incorporating portions of their finch host's song into their own display song (Payne *et al.* 1998), and female indigobirds preferentially mate with males that sing the song of their own host and lay their eggs in the nest of those same hosts (Payne *et al.* 2000), which together may result in assortative mating. Indeed, Balakrishnan & Sorenson (2006) have shown that male Cameroon indigobirds only respond aggressively to males singing the same host song, and ignore males that sing a different host song, demonstrating that males do not consider those from a different host race as competitors for mating. This provides indirect evidence that the host races of Cameroon indigobird are mating assortatively. Incorporation of components of their host's song into their own mating song may have caused sexual isolation and speciation among populations of the Cameroon indigobird.

In the above systems of exploitation via mating traits, if the exploited males and females change their mating signals and preferences in response to the cost of the interaction, then the species imposing the cost (that is, benefiting) would also be expected to coevolve along with the changes in their prey, in turn selecting for more changes in an arms race. Therefore, the coevolutionary process would be expected to continue to displace mating traits in populations sympatric with the species preying on their sexual signals and preferences compared to populations in allopatry (Thompson 2005).

Mimicry

Mimicry is another species interaction that may also directly change mating traits of a species. This can result if the traits used for mimicry are the same traits used in mate choice,

and the species mimics different model species in different areas. In this case individuals of the focal species gain benefits by mimicking the traits of another species. But with each population evolving to mimic a different model there is also the evolution of different mating traits and the potential for sexual isolation. There are at least two possible reasons why an association may arise between mimicry and mating traits. First, perfection of mimicry is important for survival and hence should be incorporated by sexual selection as an indicator of quality. Second, if there are mimetic forms, preference for an individual's own mimetic form should evolve to avoid mating with another mimetic form that would result in the production of offspring with intermediate phenotypes that do not mimic either model species (e.g., Naisbit *et al.* 2001).

Poison arrow frogs are an example of a system where mimicry may lead to speciation. The imitating poison dart frog (*Dendrobates imitator*) has different colour morphs in different regions of Peru, in each area mimicking a different sympatric poison dart frog species (Symula *et al.* 2001). A related species, the strawberry poison dart frog (*Dendrobates pumilio*), has different colour morphs and there is assortative mating among colour morphs through female choice (Summers *et al.* 1999; Reynolds & Fitzpatrick 2007). It is reasonable to suggest that the imitating poison dart frog may also use colour as a mating trait. If so, then the evolution of colour morphs in the imitating poison dart frog due to mimicry may also indicate the potential for sexual isolation among the different morphs within the one species. Such a process has been demonstrated in *Heliconius* butterflies involved in mimicry (Jiggins *et al.* 2001; Jiggins *et al.* 2004). Divergence in wing colour pattern between mimetic populations (races) of *H. melpomene*, driven by selection for predator avoidance, has incidentally resulted in a degree of assortative mating between populations (Jiggins *et al.* 2004). These mimicry examples represent a direct cross-over with other forms of ecological divergence, because the ecological trait under selection is also the mating trait, i.e. a 'magic trait' (see Box 1).

Competition for signal space

Competition for signal space may be a very common, but relatively overlooked species interaction that causes selection on mating traits. Just as the abiotic environment exerts selection on mating traits (Boughman 2002), so does the biotic environment. In sympatry with a species that overlaps in mating signal there may be selection for reducing signal interference (Taper & Case 1992; Chek *et al.* 2003; Cooley *et al.* 2006). This has been called 'noisy neighbours' and facilitated reproductive character displacement (Howard 1993; Noor 1999). It has had a history of being closely associated with reinforcement but has been applied to

species that do not hybridize (Otte 1989; Howard 1993; Noor 1999). Interacting species do not need to be related at all to cause signal interference. Reinforcement should be applied to species that mistake each other as mates, whereas competition for signal space should be reserved for situations that do not involve attempts to mate but rather signal interference. Although the idea of signal interference between species is not new, very few studies have explicitly tested for displacement of mating traits among populations, and associated levels of sexual isolation. Amézquita *et al.* (2006) found no significant displacement of male mating call in the frog *Allobates femoralis* at sites where it is sympatric with another frog, *Epipedobates trivittatus*, which exerts masking interference on call frequency. They did find, however, significant displacement in *Allobates femoralis* male receptivity to other males' calls in populations sympatric with *Epipedobates trivittatus*. The implications of this displacement for population divergence have not been tested, nor whether female preference for male call has also changed.

SPEED AND EXTENT OF DIVERGENCE

It has been suggested that to cause the large differences in mating signals often seen among closely related species, selection must be strong and rapid (Shuster & Wade 2003). The speed and extent of mating trait divergence is likely to differ depending on the type of species interaction. In exploitative species interactions (e.g. predation/parasitoidism, deceptive pollination, brood parasitism, and some types of mimicry) rapid coevolution would be expected as the exploiter causes signal changes in the exploited species, resulting in a coevolutionary chase (Gavrilets 1997). Hence, these interactions could cause rapid and on-going divergence in mating traits among populations experiencing different exploitative species interactions. Alternatively, mutualisms (e.g. some types of mimicry) are predicted to result in an equilibrium state (Gavrilets & Hastings 1998), with the stable states (equilibria) likely to be different for each population experiencing a different interaction. For interactions where species 'incidentally' interact on the basis of their mating traits (e.g. reinforcement and signal space competition), it is not expected that one species would track the evolution of the other species' mating traits; rather there would only be selection for divergence, which would ease once divergence has occurred. These non-exploitative species interactions would also cause divergence from populations not experiencing the interaction, but potentially at a slower rate and causing less divergence than that caused by exploitative species interactions.

Evidence of the speed of divergence caused by species interactions comes from two systems that have experienced selection on mating traits due to reinforcement. Higgie *et al.*

(2000) found that after only nine generations of sympatry with a closely related species male mating traits of a naïve population had diverged to the same extent as sympatric populations measured in the wild, suggesting that evolution in the wild would also operate at a rapid pace. Hoskin *et al.* (2005) showed that an isolated contact zone population of a frog lineage speciated from both the sympatric lineage and the allopatric populations of its own lineage in less than 6500 years. Both of these cases show that species interactions caused the evolution of RCD over very short evolutionary time scales. Exploitative species interactions could cause even faster divergence due to their coevolutionary nature.

RCD SPECIATION: CRITERIA AND PATTERNS OF DIVERSIFICATION

Above we have shown that RCD can be generated by numerous fundamental species interactions that directly affect mating traits. As demonstrated by recent reinforcement research, the evolution of RCD can incidentally drive sexual isolation between displaced and non-displaced populations (Fig. 1). In this sense, the degree of mating trait divergence associated with RCD may be sufficient for speciation. Alternatively, RCD may generate mating trait divergence that is then acted upon by reinforcement to complete speciation. Where species interactions generate divergent mating traits between displaced and non-displaced populations, hybrids may have intermediate mating traits. Reinforcement can be driven purely by selection against intermediate mating traits in hybrids (Vamosi & Schluter 1999; Höbel & Gerhardt 2003; Servedio 2004). Similarly, sexual selection could also elaborate differences in mating traits initiated by species interactions, causing further divergence among populations (Noor 1999; Schluter 2001).

The following criteria for demonstrating 'RCD speciation' should be addressed in order to assess the contribution of this mode of speciation vs. other factors: (1) mating traits are identified in the focal species; (2) mating traits are affected by a species interaction, such that selection on mating traits is likely; (3) species interactions differ among populations (present vs. absent, or different species interactions affecting mating traits in each population); (4) mating traits (signal and/or preference) differ among populations due to differences in species interactions; (5) speciation requires showing that mating trait divergence results in complete or near complete sexual isolation among populations. Results will be most informative in a well-resolved biogeographic setting where the relationship and history among populations is known. Further, assessment of ecological and underlying environmental differences between populations will allow clearer interpretation of results.

Because selection is acting directly on mating traits, speciation can be rapid, and can involve little more than mating traits among species. This will also result in the evolution of sexual dimorphism because mating signals are generally restricted to one sex. Such speciation is obvious in groups with mating signals conspicuous to humans (e.g. colour), but easily overlooked in groups with ‘cryptic’ mating signals (e.g. pheromones). The former have long been recognized as spectacular radiations (e.g. birds of paradise, hummingbirds), whereas the contribution of cryptic species to the diversity of many regions is being increasingly recognized (e.g. Bickford *et al.* 2007). Because RCD speciation is derived through rapid mating trait divergence, it will readily result in genetically ‘cryptic’ species that do not differ at neutral loci, and will potentially create paraphyly of the parental species (e.g. Hoskin 2007).

Species interactions on mating traits have been relatively overlooked because they can be hard to identify and quantify, and their selective effect not as easily envisaged or tested as that of, for example, the physical environment. Here, species interactions are the subset that directly affect mating traits, so knowing mating trait variation in the focal population will allow an assessment of likely candidate interactions. We suggest greater consideration of these species interactions in speciation studies. This can involve identification of interacting species likely to exert selection on mating traits of the focal species, quantification of variation in such species interactions across populations (as is done for variation in many abiotic factors), correlation between mating trait variation and interacting species presence and abundance, and tests of the degree to which mating trait variation is affected within and between populations under alternative interacting species environments. The basic approach is similar to that used for reinforcement studies – detecting changes to mating traits in populations that are sympatric and allopatric to the interacting species, where allopatric phenotypes can be considered the reference or starting point without selection imposed by the interacting species.

GEOGRAPHY OF SPECIATION

RCD speciation is most easily envisaged in species with disjunct distributions. Allopatric speciation may result between isolated populations, due to divergent selection generated by different species interactions in each and limited gene flow between them (Fig. 2). Parapatric divergence may occur where a species interacts with different species over its range, or interacts with a single species in part of its range (Fig. 2). This is particularly likely in species of broad geographic range and/or habitat tolerance. Such patterns of interaction may generate local adaptation in mating traits in the areas of overlap, and speciation between

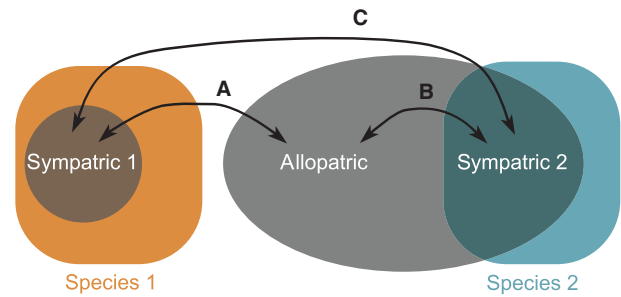


Figure 2 Geography of RCD Speciation. Populations of a focal species (grey shading) may be sympatric (darker grey) with one or more species that exert selection on mating traits, thus generating RCD in sympatric populations. This may lead to allopatric (A) or parapatric (B) speciation between sympatric and allopatric populations, or between populations sympatric with different species (C). It may also lead to sympatric speciation within a sympatric population (not shown, see text).

these displaced and non-displaced populations will be dependent on the strength of selection vs. level of gene flow at parapatric boundaries (Turelli *et al.* 2001; Gavrilets 2004).

Models of sympatric speciation generally depend on adaptation to alternate resources or habitats within a population, or more recently, selection against intermediate phenotypes in competition for continuously distributed resources (Turelli *et al.* 2001; Coyne & Orr 2004; Gavrilets 2004). The key driving force in all models is disruptive selection. Speciation from RCD could occur in sympatry where an interacting species generates disruptive selection on mating traits (Fig. 3). For example, consider a frog population in which calling frequency (male signal) ranges from 1.2 to 1.8 kHz. Invasion, range expansion or some other community perturbation introduces a frog species over the range of the population with an intermediate calling frequency, for example 1.4–1.6 kHz. Signal interference may generate disruptive selection on the mating trait of the focal species, with lower fitness of intermediate phenotypes. For another example, consider a situation in which the mating trait of a focal species is exploited by another species, and exploitation lowers fitness. Disruptive selection may result if exploitation is highest towards the middle of mating trait variation, or if exploitation is temporally restricted towards the middle of the focal species’ breeding season. Exploitation is likely to be focussed towards the mean of mating trait variation in exploitive interactions (e.g. Gray & Cade 1999). As for the signal interference example (and other readily conceivable examples from other types of interaction), intermediate phenotypes may have lower mating success and divergence in mating traits may result in the population. Divergence would be dependent on the type of female preference, and is most easily envisaged under assortative mating.

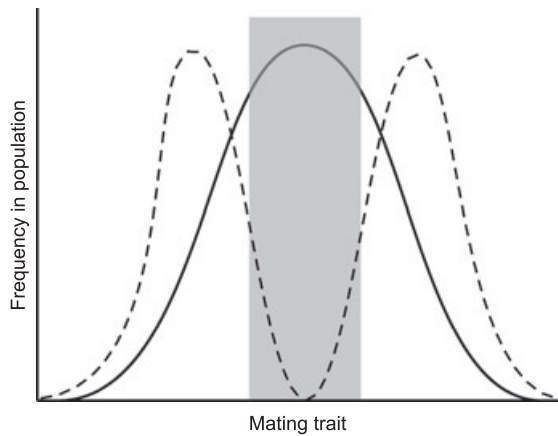


Figure 3 RCD and sympatric speciation. The solid line represents the distribution of a mating trait before selection. The mating trait may be mating signal, preference, or temporal variation in mating. The grey area represents the phenotypes directly selected against by the interacting species. As a result of this selection, the individuals with the affected phenotypes receive less matings, while those on either side receive more. This disruptive selection ultimately results in divergence of mating traits (dotted line), potentially leading to sympatric speciation.

Sympatric speciation by RCD is not easily envisaged under strong directional preference, but is more plausible where there is assortative mating or variation in preferences, such that phenotypes on either side of the disrupted area of signal variation are chosen. Following initial mating trait divergence, reinforcement may also contribute towards speciation through selection against intermediate phenotypes between the two groups (Servedio 2004). Divergence in mating traits could incidentally generate reproductive isolation on its own, without resource/habitat divergence. Alternatively, niche divergence could occur simultaneously or follow, aided by reduced gene flow associated with mating trait divergence between the two groups. Such ecological differentiation will better facilitate coexistence (Coyne & Orr 2004). Sympatric speciation by RCD is akin to 'magic trait' models of sympatric speciation (reviewed in Gavrillets 2004). Recent allopatric or parapatric speciation due to RCD should match the geographic distribution of interacting species, where these can be identified. For sympatric speciation, however, this will be more complicated.

WHERE IS RCD SPECIATION MOST LIKELY TO OCCUR?

RCD speciation is most likely where isolated populations of a species occur with or without a particular interacting species, or occur in different community assemblages. Mosaic contact zones, habitat isolates, and environmentally complex regions offer particularly conducive settings. In

mosaic contact zones, which involve a patchwork interaction between two lineages, different evolutionary outcomes can arise between isolated populations of a lineage in the contact region or between one of these isolates and the main range of the lineage, driven by the presence/absence of reinforcing selection or different outcomes of reinforcing selection in different isolates (Howard 1993; Hoskin *et al.* 2005). Habitat isolates (e.g. islands, mountain tops) offer a likely setting because species composition may vary greatly between isolates, thus exposing populations in each to different community interactions. Populations that colonize offshore islands may diverge from mainland populations through sexual selection in the absence of key species interactions in depauperate island communities.

Environmentally complex regions (e.g. New Guinea, Central/South America, and the heathlands of South Africa and south-western Australia) offer a particularly conducive setting because the degree or scale of variation in physical features (e.g. topography, soils, moisture) is typically reflected in species with small and patchy distributions, and high species turnover (Buckley & Jetz 2008). The resulting mosaic of species interactions across populations of species could provide a powerful engine of diversification. A feedback process can be envisaged where diversity then generates an increasingly conducive setting for further diversification, resulting in radiations of similar species. An obvious complication is the degree to which divergence among populations is driven by adaptation to environments differing in species interactions vs. underlying habitat, or both. Situations in which divergence appears primarily restricted to mating traits are insightful in this regard.

Community rearrangements associated with environmental perturbations, for example glaciation and global climate changes during the Quaternary, may have driven RCD speciation. These periods greatly altered distributions, population connectivity and community structures, hence exposing populations to selection pressures from novel and heterogeneous communities (McPeck & Gavrillets 2006). Range expansions, introductions of new species, or removal of species from a community can alter selective pressures on mating traits experienced by a particular population. Such community changes have always occurred for a variety of reasons but have been recently exaggerated by human activities. This is not an exhaustive list and resolution requires further integration of evolutionary biology, community ecology, and conservation biology.

CONCLUSION

Sexual selection generates mating preferences and signals, but other processes such as species interactions may be of greater importance in causing among population divergence in these mating traits. We suggest that: (1) a diverse array of

fundamental species interactions beyond reinforcement can generate a pattern of reproductive character displacement, and (2) this divergence in mating traits among populations within a species can generate sexual isolation, and potentially speciation. Therefore, species interactions that generate direct selection on mating traits can drive rapid speciation when such interactions differ among populations. Extending this idea, a novel species interaction that affects mating traits of a population can potentially initiate or drive sympatric speciation. This can generate species that differ in little other than mating traits, a pattern generally attributed to speciation by sexual selection.

We urge further consideration of species interactions based on mating traits in speciation research. The potential for such biotic interactions should be factored into empirical studies in suitable systems, and there are clear avenues for experimental and theoretical analysis of the process under different forms and settings of species interaction. RCD speciation is not easily demonstrated as it is a potentially rapid process (and so key patterns will be quickly obscured), species interactions are not easily quantified and tested, and detailed criteria must be demonstrated to disentangle the process from other mechanisms of divergence. Nonetheless, as shown by reinforcement research, the process is tractable under the right settings and conditions.

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