

<Review>

Asymmetry in Reproductive Character Displacement

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ABSTRACT: A commonly held view in studies of character displacement is that character states of both species are shifted in areas of sympatry. This view has been confirmed in an overwhelming number of cases for ecological character displacement. Excluding species pairs in which one of the two interacting species is found only within the distribution of the other species and species displaying gynogenesis, the pattern of reproductive character displacement is asymmetrical in that the shift in character states between areas of sympatry and allopatry occurs in only one of the two interacting species. Hypotheses for the reasons behind this asymmetry in reproductive character displacement include (1) homogenization by gene flow, (2) other mechanisms of reproductive isolation, and (3) sufficient reproductive isolation being provided by one of the interacting species exhibiting a pattern of reproductive character displacement. Because reproductive isolation can be achieved by divergence at any point in a sequence of premating reproductive behaviors and postmating developments, it is necessary to understand the mechanisms of reproductive isolation of two interacting taxa in areas of sympatry and allopatry and to analyze the relative contributions of potential factors to reproductive isolation to disentangle hypotheses for the patterns of asymmetry.

Key words: *Gryllus fultoni*, *Gryllus vernalis*, Reproductive character displacement, Reproductive isolation

INTRODUCTION

Closely related species occurring at the same time and location may interact with each other ecologically or reproductively. Reproductive character displacement (RCD) is a pattern in which characters that promote reproductive isolation of closely related species are more dissimilar in sympatry than in allopatry (Brown and Wilson 1956, Grant 1972, Howard 1993, Gerhardt and Huber 2002). Selection against costly interspecific mating (Dobzhansky 1940, Howard 1993, Butlin 1995), which is assumed to be less likely when traits involving mate choice diverge, has been termed reinforcement (*sensu* Blair 1955) and may contribute to speciation (Servedio and Noor 2003). In the last two decades there has been a surge of interest in studies of reinforcement and RCD. Such interest stems from the fact that several theoretical approaches have shown the feasibility of reinforcement (Liou and Price 1994, Kelly and Noor 1996, Servedio and Kirkpatrick 1997, Kirkpatrick and Servedio 1999, Kirkpatrick 2000) and the accumulating empirical evidence for both reinforcement and RCD (see Table 1 in Gabor and Ryan 2001, Gerhardt 1994, Marshall and Cooley 2000, Gabor and Ryan 2001, Höbel and Gerhardt 2003, Jang and Gerhardt 2006a, Jang and Gerhardt 2006b, Jang and Gerhardt 2007).

Like RCD, ecological character displacement (ECD) is expected to evolve in response to an interaction between sympatric taxa

(Brown and Wilson 1956, Grant 1972). In ECD, however, the traits in question serve to reduce interspecific competition for resources (Grant 1972). Competition leads to divergence in the resources used or the ways that the resources are acquired, e.g., different bill sizes or shapes in birds (Schluter et al. 1985). Reproductive isolation is thought to occur as a by-product of genetic divergence between populations occupying different habitats (Dodd 1989, Kirkpatrick 2001, Albert and Schluter 2004).

A common theoretical expectation about both kinds of character displacement is that character states of both species will be shifted and therefore contribute to divergence in areas of sympatry (Fig. 1; see Fig. 2 in Grant 1972). This classical pattern is evident in numerous examples of ECD. In a set of 61 published cases of character displacement reviewed by Schluter (2000a, 2000b), the most common pattern reported was exaggerated divergence in sympatry, wherein phenotypic differences between two or more species are greater where the species coexist than where they occur separately (Schluter 2000a, Schluter 2000b). Less frequently observed are patterns of “community-wide character displacement” and “species-for-species matching”. Community-wide character displacement is the overdispersion of trait means, a pattern in which the mean phenotypes of ecologically similar species tend to be evenly spaced along a size or other phenotypic trait axis (Strong Jr. et al. 1979, Marchinko et al. 2004, Dayan and Simberloff 2005). Species-for-species matching is unusually similar guild structures or phenotype distributions

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between sets of species that have evolved independently. Because it is difficult to compare divergence of traits between areas of allopatry and sympatry, the latter two patterns of character displacement are not considered in this paper.

Excluding species pairs in which one of the two interacting taxa is found only within the distribution of the other species (McLain and Rai 1986, Noor 1995, Higgie et al. 2000, Höbel and Gerhardt 2003) and gynogenetic mollies, *Poecilia formosa*, in which males do not exist (Gabor and Ryan 2001), the pattern of RCD is invariably asymmetrical in that the trait of interest differs significantly between sympatry and allopatry in only one of the two interacting species (Cooley 2007). In the congeneric species pairs in Table 1, traits of the first taxon showed a distinct shift in areas of sympatry, whereas the corresponding traits of the second taxon showed a smaller shift or no difference between sympatric and allopatric populations. The situation was more complicated in the pied flycatcher (*Ficedula hypoleuca*) and the collared flycatcher (*F. albicollis*), which have overlapping breeding distributions in Central and Eastern Europe (Sætre et al. 1997). Song characters showed asymmetry in RCD (shift in collared flycatcher but not in pied flycatcher; Haavie 2004) but male plumage characteristics did not (Sætre et al. 2003).

While most examples of asymmetry in RCD involve acoustic characters, there are also robust examples of asymmetry in RCD in nonacoustic characters. Spawning in Pacific sea urchins (genus *Echinometra*) occurs by release of gametes into the water, and reproductive isolation between closely related species depends on the gamete recognition protein "bindin", which attaches sperm to eggs. The distribution of bindin alleles differs dramatically between sympatric and allopatric populations of *E. oblonga*, whereas the bindin

alleles of *Echinometra* sp. C exhibited almost no geographic differentiation between sympatric and allopatric populations (Geyer and Palumbi 2003). There is strong support for the hypothesis that divergence in the bindin protein in sympatric populations of *E. oblonga* is driven by selection.

Asymmetry in RCD has also been documented in olfactory signals. Two subspecies of the house mouse, *Mus musculus musculus* and *M. m. domesticus*, hybridize in contact zones that extend from

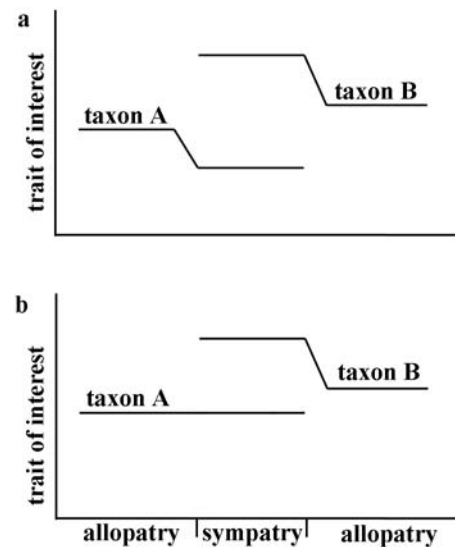


Fig. 1. Patterns of character displacement. The traditional view of character displacement is that character states of both taxa (A and B) diverge in areas of sympatry (a). In an asymmetrical pattern of RCD, the trait of interest is shifted in only one (B) of the two interacting taxa in sympatry (b).

Table 1. Examples of asymmetry in reproductive character displacement. In congeneric species pairs, traits of taxon A showed a distinct shift in areas of sympatry, whereas the corresponding traits of taxon B showed a smaller difference between sympatric and allopatric populations.

Trait	Organism	Taxon A	Taxon B	Reference
Acoustic signal	Tree frogs	<i>Litoria verreauxii</i>	<i>L. ewingii</i>	Littlejohn 1965
	Chorus frogs	<i>Pseudacris feriarum</i>	<i>P. nigrita</i>	Fouquette 1975
	Toads	<i>Gastrophryne carolinensis</i>	<i>G. olivacea</i>	Loftus-Hills and Littlejohn 1992
	Cicadas	<i>Magicicada neotredescim</i>	<i>M. tredescim</i>	Marshall 2000, Cooley et al. 2006
	Crickets	<i>Gryllus fultoni</i>	<i>G. vernalis</i>	Jang and Gerhardt 2006b, Jang and Gerhardt 2007
	Flycatcher	<i>Ficedula albicollis</i>	<i>F. hypoleuca</i>	Haavie et al. 2004
Recognition protein	Sea urchins	<i>Echinometra oblonga</i>	<i>E. sp. C</i>	Geyer and Palumbi 2003
Olfactory signal	House mouse	<i>Mus musculus musculus</i>	<i>M. m. domesticus</i>	Smadja et al. 2004, Smadja and Ganem 2005
Cuticular hydrocarbons	Fruit fly	<i>Drosophila serrata</i>	<i>D. birchii</i>	Blows and Allan 1998

Denmark to the Caucasus. The house mouse uses urinary signals to communicate information about individual identity, population, and mate choice (Coopersmith and Lenington 1992, Smadja and Ganem 2002). Mate preferences were significantly higher in the contact zone than in allopatry in both subspecies (Smadja et al. 2004). However, patterns of preference were stronger in *M. m. musculus* than in *M. m. domesticus* (Smadja et al. 2004, Smadja and Ganem 2005). Here I discuss possible explanations for asymmetry in RCD in general.

HYPOTHESES FOR ASYMMETRY IN RCD

Hypotheses about the reasons for asymmetry in RCD include (1) homogenization by gene flow (Liou and Price 1994), (2) the effectiveness of mechanisms of reproductive isolation other than the traits examined for RCD, and (3) the adequacy of divergence of mate-identification in traits of the taxon that exhibits a pattern of RCD to enforce reproductive isolation in both taxa. One or more of these hypotheses may help to explain this and other examples of asymmetry in RCD.

The first hypothesis states that the lack of RCD in one species may be attributed to gene flow between sympatric and allopatric populations, which homogenizes whatever divergence is created by local selective pressures (Pfennig and Ryan 2006). Such homogenization can occur if there is little or no geographical barrier between areas of sympatry and allopatry. Gene flow may be at its maximum if either allopatric or sympatric areas adjacent to areas of sympatry are relatively small. However, the effect of gene flow is generally dilution, rather than elimination, of divergence created by selection (Liou and Price 1994, Pfennig and Ryan 2006). *Drosophila pseudoobscura* exhibits high intraspecific gene flow (Noor and Smith 2000), yet females express divergent mating behaviors in sympatric and allopatric populations (Noor 1995, Noor and Ortíz-Barrientos 2006).

Allopatric populations of *Gryllus vernalis* (Orthoptera: Gryllidae) are generally located close to sympatric populations and there are no obvious barriers to dispersal between areas of sympatric and allopatry (Jang and Gerhardt 2006a). Thus, the homogenization-by-gene-flow hypothesis may be able to account for the absence of divergence in calling song characters between sympatric and allopatric *G. vernalis* populations. However, this hypothesis is inadequate to explain the direction of asymmetry in RCD in other pairs of species, such as the Australian treefrogs, *Litoria ewingii* and *L. verreauxii*. The allopatric zone of *L. ewingii* is diverse and includes Tasmania, which is separated from the mainland area of sympatry with *L. verreauxii* in southeastern Australia by the Bass Strait (Littlejohn 1965), whereas the sympatric and allopatric areas of *L. verreauxii* are often adjacent. However, the pulse rates of calls of

L. ewingii from allopatric populations (76.7 pulses/s; Littlejohn 1993) are only 11.3% higher than those of sympatric populations (68 pulses/s) compared with a difference of 63% in the pulse rates of calls of *L. verreauxii* (137.7 pulses/s in sympatric populations versus 84.3 pulses/s in allopatric populations) (Littlejohn 1999). The gene flow hypothesis would predict the opposite pattern of asymmetry in RCD in this pair of treefrogs. Smadja and Ganem (2005) speculated that past asymmetrical gene flow may have caused the asymmetrical pattern of RCD in mate preference between two subspecies of the house mouse. There is evidence for aggressive dominance of male *M. m. domesticus* over *M. m. musculus*. *M. m. domesticus* may immigrate into *M. m. musculus* populations, whereas movement in the reverse direction may be hindered by aggression from *M. m. domesticus* (Smadja and Ganem 2005). This selective pressure favors the expression of stronger mate preferences in both sexes of *M. m. musculus* than in *M. m. domesticus*.

The second hypothesis is that reproductive isolation is achieved by cues other than the sexual signals being analyzed in the taxon that does not exhibit RCD. Indeed, there may be no actual asymmetry if different mechanisms make conspecific mate identification equally effective in both taxa. Within the realm of acoustic signaling, for example, each member of a pair of closely related, sympatric taxa may use entirely different acoustic criteria (review in Gerhardt and Huber 2002). Reproductive isolation may also be achieved using different sensory modalities in different taxa or populations. For example, Ortíz-Barrientos et al. (2004) found that *D. pseudoobscura* females in areas of sympatry displayed increased discrimination against *Drosophila persimilis* males based on odor, rather than male song, which is the mechanism used in allopatry. The flycatcher example described above is another example of RCD using signals in different modalities. In addition, the results of a study of close-range mating behaviors indicated that females of sympatric *G. vernalis* populations were much less likely to mount heterospecific males than allopatric females (Jang et al. 2007), suggesting that there is differentiation in the chemotextile structures of antennae or courtship songs between sympatric and allopatric populations of *G. vernalis* or that females in sympatric, but not allopatric, populations might use these cues for close-range mate choice. Thus reproductive isolation in *G. vernalis* vis-à-vis *G. fultoni* may rely primarily upon close-range mating behaviors, while it is as yet unclear whether sympatric and allopatric populations of *G. vernalis* differ in their close-range mating behaviors.

The last hypothesis is that an isolating mechanism in one species is usually sufficient to enforce reproductive isolation between two interacting taxa. When divergent taxa reestablish contact, the conventional assumption is that selection for assortative mating is bidirectional between the two taxa. However, the strength of selection

on the two species may differ because of differences in their ecology, demography, or evolutionary history. For example, Cooley et al. (2006) speculated that the relative abundances of species interacting in contact zones also may lead to displacement asymmetries. In all sympatric populations, *G. vernalis* is much more numerous than *G. fultoni* (Jang and Gerhardt 2006a). Thus, the selection pressure promoting positive assortative mating would be greater in *G. fultoni* than in *G. vernalis* (Bordenstein et al. 2000), which should increase the probability that enhancement of reproductive isolation has evolved mostly in *G. fultoni*. This explanation is also consistent with Littlejohn's (1993) suggestion that selection pressure for reproductive isolation may be greater on the species that is expanding its range of distribution into that of the other species because the relative numbers of the invading taxon are likely to be lower than those of the established taxon.

TESTING THE HYPOTHESES

The most critical information for documenting RCD is whether or how much the pattern of differentiation observed provides reproductive isolation between interacting taxa. Levels of hybridization are typically measured to estimate reproductive isolation between taxa in sympatry. However, hybridization data alone are often misleading because laboratory and field studies of hybridization can produce very different results (Smith and Cade 1987, Cade and Tyshenko 1990, Gray and Cade 2000) and because these data do not reveal how reproductive isolation is maintained. Therefore, the factors that drive the divergence between closely related taxa in areas of sympatry must be identified. Identifying patterns of character displacement, both symmetric and asymmetric, can be secondary after determining the factors that may have evolutionary consequences for reproductive isolation.

To address the homogenization hypothesis for asymmetry in RCD, researchers will require information on gene flow between sympatric and allopatric populations in a taxon. If there is substantial gene flow between sympatric and allopatric populations, all populations across the zone of sympatry and allopatry will evolve together (Slatkin 1994), thus resulting in no RCD. However, if there is little gene flow, each population evolves more-or-less independently, which may lead to genetic differentiation between sympatric and allopatric populations, and a pattern of RCD. To test the second and third hypotheses for the causes of asymmetry in RCD, researchers must conduct comprehensive behavioral studies of premating reproductive isolation, which can be achieved by interrupting any point in a whole range of courtship and mating sequences. It is unlikely that a single factor is responsible for reproductive isolation between closely related taxa in sympatry in most cases. A judicious approach

would be to analyze the relative contributions of potential factors to reproductive isolation (Tregenza 2002), which may ultimately reveal the underlying mechanisms that produce asymmetric patterns of RCD.

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