

Decoding Asymmetries in Reproductive Character Displacement

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ABSTRACT.—Reproductive Character Displacement (RCD) has long been of interest to evolutionary biologists because of its association with speciation and reproductive isolation. Most studies of RCD focus on only a single species; however, when information about the evolutionary responses of two species is available, a possible pattern emerges: RCD often appears to be asymmetrical. Possible causes of displacement asymmetries are varied and include asymmetrical costs of hybridization, constraints, the effects of relative abundance, and extinction. Yet in spite of this variety, further study may show that asymmetries in RCD contain important clues about the interactions of species in contact zones.

Keywords: Reproductive character displacement, speciation, hybridization, gene flow, mating signals

INTRODUCTION

Historically, contact zones have been thought of as “natural laboratories” for studies of speciation processes (Hewitt, 1988; Harrison, 1990). One of the most interesting and controversial interactions between overlapping species is reproductive character displacement (RCD), in which sympatric (overlapping) populations show exaggerated differences in reproductive characters (often morphological, chemical, or behavioral sexual signals) relative to allopatric (non-overlapping) populations. Because RCD is one outcome of selection to reduce the likelihood of heterospecific sexual interactions, it may provide important clues concerning the nature and origins of reproductive isolation. Schluter’s (2000) review of ecological character displacement (ECD) suggests that displacement asymmetries can provide clues about past competitive inequalities. These asymmetries are, in effect, “fossils” of past selection, reflecting competitive inequalities that are no longer immediately apparent or that have been obscured by subsequent evolutionary change (Grant, 1972; Schluter, 2000).

What might a similar survey of the reproductive character displacement literature show? RCD literature that includes explicit information about the responses of both taxa involved remains surprisingly scarce and can be summarized in a relatively modest table (Table 1). Yet these few studies hint at a pattern: One taxon typically shows more displacement than the other, and in some cases, all displacement seems to occur in only one taxon (see Fig. 1). Is this pattern of asymmetrical displacement just an artifact of methodological bias or small sample size? Or, are patterns of asymmetry reflections of the processes responsible for RCD? The existing RCD literature—aneecdotal though it is—suggests that asymmetries could be produced by un-

equal hybridization costs, biases in likelihood of hybridization, asymmetrical effects of reproductive interference, evolutionary constraints, or historical accidents. Furthermore, even though data are scant, it may be possible to distinguish among some of these causes. The following discussion serves to highlight how displacement asymmetries might provide important insights into RCD and underscore the importance of obtaining additional data.

What is reproductive character displacement?

The term reproductive character displacement (RCD) has been used in different ways by different authors, and many of the differences reflect a desire to separate evolutionary processes and patterns. Brown and Wilson (1956) defined reproductive character displacement as a biogeographic pattern in which inter-species (or inter-population) differences in sexual characters are exaggerated in sympatry, relative to their condition in allopatric populations. Similarly, Howard (1993) considers RCD to be simply a pattern of character expression, while Littlejohn (1981) uses the terms RCD and “reinforcement” interchangeably to describe both process and pattern. Butlin (1987; 1989) applies the term RCD to cases in which two interacting taxa show a pattern of displacement and are incapable of exchanging genes, and he reserves the term “reinforcement” for cases in which gene flow is possible. I will use the term “reproductive character displacement” to refer to a general biogeographic pattern in which the reproductive isolation of species is enhanced in sympatry, because this more general definition makes no *a priori* assumptions about gene flow.

Intrinsic causes: Selection and Constraints

Most theoretical treatments of RCD agree that restrictions on gene flow play a strong role in whether or not se-

lection leads to displacement (Littlejohn, 1981; Sanderson, 1989; Howard, 1993; Rice & Hostert, 1993; Liou & Price, 1994; Hostert, 1997; Servedio & Kirkpatrick, 1997; Noor, 1999; Morgan-Richards & Wallis, 2003; Pfennig, 2003; Sadedin & Littlejohn, 2003; Servedio & Noor, 2003). Some studies explicitly link asymmetrical gene flow to asymmetrical RCD (e.g., Hoskin *et al.*, 2005; Peterson *et al.*, 2005). Another approach is to consider asymmetries in the costs associated with hybrid matings. Members of one species exclusively bear the costs of hybrid matings in contact zones involving the diploid, gynogenetic (exclusively female) fish species *Poecilia formosa*, whose females must spawn with males (by necessity, heterospecifics) in order to induce embryogenesis (without sexual fertilization; Ryan *et al.*, 1996; Gabor & Ryan, 2001; Gabor *et al.*, 2005). This gynogenetic sexual parasite suffers no costs of hybridization and exhibits no RCD, but its victims (*P. latipinna* or *P. mexicana*) exhibit RCD in patterns of male choosiness, suggesting a relationship between asymmetrical costs of hybridization and asymmetrical displacement.

However, there is no clear linkage between cost and displacement asymmetries in contact zones between the spadefoot toads *Spea bombifrons* and *S. multiplicata*. On the basis of call variation, RCD appears to be asymmetrical, with change evident only in *S. bombifrons* (Pfennig & Murphy, 2000; K. Pfennig, pers. comm.). Selection against hybridization also appears to be asymmetrical; in large, persistent breeding ponds, both species appear to be under selection to avoid hybridization, while in ephemeral ponds, *S. bombifrons* females are under selection to accept or even prefer heterospecific mates because hybrid tadpoles develop more rapidly than do *S. bombifrons* tadpoles (Pfennig & Simovich, 2002). But this asymmetrical selection does not appear to be reflected in displacement asymmetries: *S. bombifrons* shows the greater degree of displacement even though members of this species sometimes benefit from hybridization.

Costs could be further distorted by sex- and species-specific differences in promiscuity or discrimination ability, which affect the likelihood of hybridization and each species' exposure to the costs of hybridization. Few studies of RCD include enough detail to test these relationships, though obvious candidates include any example in which one of the possible reciprocal crosses ends in courtship failure (e.g. Noor *et al.*, 2001; Shaw & Lugo, 2001; Gabor *et al.*, 2005).

Other kinds of selection, besides those directly involving hybridization costs, can produce patterns of RCD and may commonly lead to asymmetries. Reproductive interference between two sympatric taxa with similar or overlapping sexual signals can lead to RCD in the absence of hybridization or direct sexual contact, because the presence

of a confusingly similar species reduces mate-location efficiency (Birch, 1957). The phenomenon of RCD mediated by reproductive interference has much in common with ecological character displacement (ECD), in which divergence in ecological requirements is driven by competition for shared resources; in the case of reproductive interference, the "resource" the taxa compete for is access to a particular signal channel. While the literature discussing RCD is sparse, the literature on ECD is informative and suggests that the competitive abilities of species are rarely equal and that competitive differences commonly lead to asymmetries in ECD (Grant, 1972; Schluter, 2000; Pfennig & Murphy, 2003). By extension, if the competitive interactions involved in reproductive interference are typically asymmetrical, (see Lemmon *et al.*, 2004), then asymmetries in RCD should be common.

One study that explicitly discusses this aspect of asymmetrical RCD involves call pitch displacement in periodical cicadas (*Magicicada* spp.; Cooley *et al.*, 2006). Male calls in some of these species are nearly pure-toned, with a terminal downsweep portion that elicits female acceptance signals (Cooley & Marshall, 2001). Pre-displacement, the downsweep element of the higher pitched species (*M. neotredicim*) would have been obscured by the calls and choruses of the other species (*M. tredicim*), whereas the reverse would not have been true (Cooley *et al.*, 2006). Although playback experiments to date have yielded only equivocal support for the hypothesis that reproductive interference is the cause of RCD in *M. neotredicim*, the observed asymmetry of displacement (with all of the song pitch displacement in *M. neotredicim* and none in *M. tredicim*) matches the expectation that the greatest displacement is found in the species whose calls are most severely affected by heterospecifics (Cooley *et al.*, 2006).

Constraints on character evolution might also lead to displacement asymmetries. The relationship between signalers and receivers may limit their ability to evolve independently, such as when the evolution of male call pitch is limited by female hearing sensitivity and pitch discrimination ability. Patterns of RCD between the microhylid toads *Gastrophryne olivacea* and *G. carolinensis* seem to reflect such limiting constraints: Anuran pitch perception seems limited to sounds 5 kHz and below (Fay, 1988), which constrains call evolution. The species *G. olivacea* has a call pitch that is relatively high for an anuran (≈ 4.4 kHz), and where this species is sympatric with the similar, but lower-pitched, species *G. carolinensis*, all displacement takes the form of a lowering of call pitch in *G. carolinensis* (Loftus-Hills & Littlejohn, 1992), perhaps because any further increase in *G. olivacea* call pitch would make their calls difficult for females to detect. Such "variance" constraints suggest a prediction: Constraints due to lack of variation

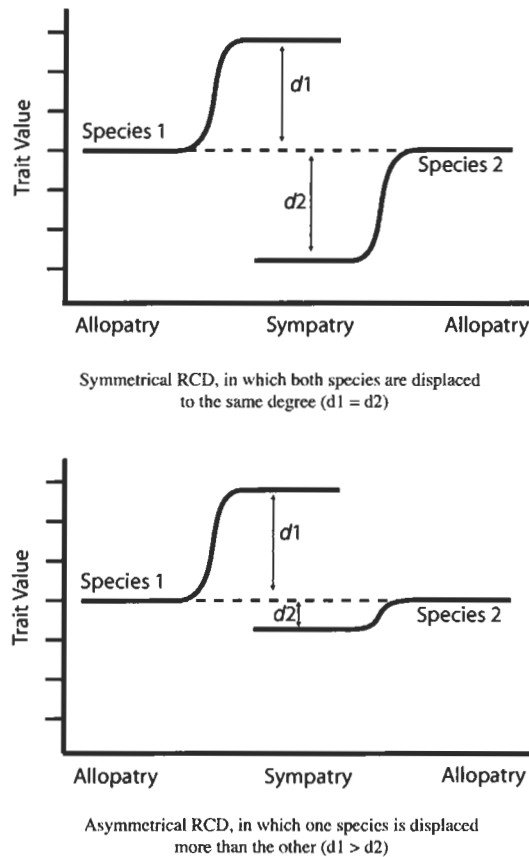


Figure 1. Schematic of displacement between two species. (A) Symmetrical RCD, in which both species are displaced to the same degree ($d_1 = d_2$). (B) Asymmetrical RCD, in which one species is displaced more than the other ($d_1 > d_2$).

are not absolute; thus, where such constraints have been overcome (and where one taxon shows an unexpected degree or direction of displacement asymmetry), then at least one of the taxa involved must necessarily be an outlier among its relatives, and it should be easily identified as such.

Waage's (Waage, 1979) study of the damselflies *Calopteryx maculata* and *C. aequabilis* suggests that limits on the intensity of pigmentation might correspond to displacement asymmetries. Wing tip pigmentation is used by both species in mate recognition; wing tips are nearly black in *C. maculata*, while they are lighter in *C. aequabilis*. In sympatry, these two species show a pattern of RCD, and as expected, the relative paleness of *C. aequabilis* wing tips is exaggerated, while the extremely dark wing tips of *C. maculata* are not significantly darker, perhaps because no further exaggeration is possible. Such "limit" constraints are likely less readily overcome by selection, and cases of

asymmetrical RCD in which they have been overcome would seem to be unlikely.

Extrinsic factors: Abundance and Historical Accident

Extrinsic causes, largely unrelated to the qualities of the species involved, might also promote asymmetries in displacement. If one species is rare relative to another, members of each species will be confronted with differing probabilities of hybridization or differing intensities of cross-species interactions, and while selection on the more abundant species may be relaxed, selection on the rarer species may be intensified. Abundance effects must be among the most difficult sources of asymmetrical RCD to detect and characterize, because abundance differences are ephemeral and leave few traces. Even so, several examples of asymmetrical RCD suggest a role for abundance differences. Two jewel wasp species, *Nasonia longicornis* and *N. vitripennis*,

have contact zones in which *N. longicornis* is relatively rare. Perhaps because they have greater exposure to heterospecifics, *N. longicornis* females appear to discriminate more strongly against heterospecifics than do *N. vitripennis* females (Bordenstein *et al.*, 2000). Range and abundance differences could also explain variation in the strength of RCD among populations of the damselfly *Calopteryx splendens* (Tynkkynen *et al.*, 2004), and they are also a partial explanation for gene flow asymmetries among some Hawaiian *Drosophila* (Kaneshiro, 1976; 1980; 1983).

Historical accidents, extinctions, or range changes might also create the appearance of asymmetries in RCD. Patterns of RCD are usually identified by noting differences between populations within and outside contact zones; however, range shifts, gene flow, or extinction can obscure these differences (Littlejohn, 1971; Walker, 1974; Otte, 1989). Historical effects might create situations in which contemporary allopatric and supposedly undisplaced populations are, in fact, both descended from displaced overlap-zone populations following the loss of "true" allopatric populations, creating the false impression that a case of RCD is asymmetrical. The problem of missing populations might be particularly acute for northern hemisphere species, because recent, dramatic climate changes associated with deglaciation might have erased or edited many preexisting patterns of RCD, obscuring the linkage between current patterns and evolutionary history. Some studies note the possibility of false or misleading asymmetries in RCD: Apparent RCD asymmetries in sea urchins (Geyer & Palumbi, 2003) and toads (Loftus-Hills & Littlejohn, 1992) could be the results of extinction or missed sampling of historically allopatric populations.

CONCLUSIONS

Are asymmetries in RCD "fossils" of past selection? Asymmetries have the potential to reveal general information about RCD, reproductive isolation, and speciation, because some of the possible causes of such asymmetries may leave tell-tale signatures. Many examples of RCD involve changes in multiple characters (Table 1), and differences in the degree or direction of displacement among these characters are common. Extrinsic factors, such as abundance effects or historical accidents, cannot readily explain the apparently independent evolution of multiple characters, and so such examples may be better explained by intrinsic differences in selection intensity, constraints, or competitive abilities.

Abundance effects have another revealing characteristic: they may be repeatable or reversible. A change in species abundance should change the outcome of species

interactions and perhaps the direction or degree of asymmetry. Although experiments testing the influence of abundance on displacement asymmetry may not be feasible, natural variations may lead to "natural experiments" that reveal the effects of abundance differences on RCD. In his study of Australian tree frogs, Littlejohn (Littlejohn, 1965) suggested that abundance differences could explain different intensities of displacement between eastern and western contact zones, although as noted above, the different degrees or directions of displacement among different characters rule out an exclusive role for abundance effects. Noor (1995) studied variations in mate acceptance criteria suggestive of RCD in *Drosophila persimilis* and *D. pseudoobscura*. Different local sympatric populations of these species appear to have responded to contact in different ways; in some cases, the mate acceptance criteria of *D. persimilis* are strongly displaced in sympatry, and in other cases they are less strongly displaced. Noor attributes these differences in displacement asymmetry differences in the relative abundances of the species at first contact, because *Drosophila persimilis* appears most strongly displaced when rare.

How might misleading asymmetries due to historical effects be identified? Only a complete extinction of one allopatric, undisplaced population, followed by a recolonization from sympatric, displaced populations will both preserve a partial pattern of RCD and create a misleading asymmetry. Thus, examples in which there is a pattern of partial asymmetry, in which both taxa change, but one changes more than the other, or patterns in which different degrees or directions of asymmetries are seen in different characters, are unlikely to be attributable to recolonization following extinction.

Are there any other patterns of asymmetry that could unlock some of the clues embedded in RCD? At present, the sparseness of the literature prevents strong conclusions and challenges us with basic questions: Given the role of selection in RCD, should we ever expect anything but asymmetries in RCD? Is symmetrical displacement an inappropriate and unrealistic null model for such evolved patterns? Finally, will future studies reveal useful generalizations, or are the generalizations noted above just so much unsupported—and unsupported—speculation?

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Table 1. Published examples of divergent RCD that include details of the degree of displacement of both interacting taxa. Studies that measure only likelihood of crossmating or that do not allow an assessment of the relative changes in both taxa (e.g. Saetre *et al.*, 1997; Pfennig & Simovich, 2002) are not included. "Trait" is the trait displaced; "Ratio A" is the ratio of the highest trait value relative to the lowest trait value in one taxon; "Ratio B" is the same value for the other taxon. For example, if displaced (sympatric) populations of Taxon A have a trait value of 2, while undisplaced (allopatric) populations have a value of 1, "Ratio A" would be 2. Similarly, if displaced populations of Taxon B had a trait value of 0.5, while undisplaced populations had a value of 1, "Ratio B" would also be 2. "Symmetry" is calculated as the log of the greater of Ratio A or Ratio B, divided by the log of the lesser of these values; as such, it gives an approximate indication of displacement symmetry (Schluter, 2000). For each species pair, or for each character within a species pair, the more displaced taxon is indicated by bold text or by an asterisk. Table modeled after Table 6.1 of Schluter (Schluter, 2000).

Taxon and source	Trait	Species A Ratio	Species B Ratio	Symmetry Index
Tree frogs				
Littlejohn 1965		<i>Litoria (Hyla) ewingi</i>	<i>L. verreauxi</i>	
	Pulse duration	1.17	1.00	0.00
	Dominant frequency	1.01	1.04	0.25
	Pulse rate	1.13	1.45	0.33
	Pulses per note	1.33	1.41	0.83
Chorus frogs				
Fouquette 1975		<i>Pseudacris nigrita</i>	<i>P. feriarum</i>	
	Pulse rate	1.00	1.69	0.00
	Pulses per note	1.11	1.38	0.33
	Dominant frequency	1.06	1.07	0.86
Tree frogs				
Ralin 1977		<i>Hyla chrysoscelis</i> (W)	<i>H. versicolor</i>	
	Call duration	1.10	1.03	0.31
	Call pulse rate	1.03	1.06	0.51
		<i>Hyla chrysoscelis</i> (E)	<i>H. versicolor</i>	
	Call duration	1.05	1.03	0.61
	Call pulse rate	1.07	1.06	0.86
Solanaceae				
Whalen 1978		<i>Solanum grayi</i>	<i>S. lumholtzianum</i>	
	Large anther length	1.61	1.00	0.00
	Style length	1.42	1.01	0.03
Damselflies				
Waage 1979		<i>Calopteryx maculata</i>	<i>C. aequabilis</i>	
	Female wing transparency (light portion)	2.13	1.23	0.27
	Female wing transparency (dark portion)	1.24	2.02	0.31
	Female front wing length	1.13	1.16	0.82
Crayfish				
Butler 1988		<i>Orconectes sanbornii</i>	<i>O. rusticus</i>	
	Male carapace length	1.08	1.03	0.38
	Female carapace length	1.1	1.05	0.51
Ground crickets				
Benedix and Howard 1991		<i>Allonemobius fasciatus</i>	<i>A. socius</i>	
	Call pitch (East zone)	1.02	1.00	0.00
	Call pitch (West zone)	1.01	1.00	0.00
	Inter-chirp interval (East zone)	1.06	1.00	0.00
	Inter-chirp interval (West zone)	1.03	1.00	0.00
	Pulse rate (East zone)	1.01	1.00	0.00
	Pulse rate (West zone)	1.08	1.00	0.00
Toads				
Loftus-Hills & Littlejohn 1992	Call pitch	<i>Gastrophryne carolinensis</i>	<i>G. olivacea</i>	0.00
		1.10	1.00	
Amazon mollies				
Ryan <i>et al.</i> 1996 [26]	Proportion of heterospecific courtships	<i>Poecilia latipinna</i>	<i>P. formosa</i> (gynogenetic)	0.00
		3.00	1.00	

Table 1 continues ->

Table 1 (continued)

Taxon and source	Trait	Species A Ratio	Species B Ratio	Symmetry Index
13-year periodical cicadas				
Marshall and Cooley 2000	Call pitch	<i>Magicicada neotredecim</i> 1.31	<i>M. tredecim</i> 1.00	0.00
Rhinoceros beetles				
Kawano 2002	Head horn length (both morphs)	<i>Chalcosoma atlas</i> 1.14	<i>C. caucasus</i> 1.06	0.44
	Body length (both morphs)	1.10	1.06	0.61
	Genitalia length (both morphs)	1.14	1.12	0.86
Stag beetles				
Kawano 2003	Mandible length	<i>Odontolabis cuvera</i> 1.01	<i>O. mouhoti</i> 1.08	0.13
	Body length	1.11	1.04	0.38
	Genitalia length	1.09	1.06	0.68
Sea urchins				
Geyer and Palumbi 2003	Bindin allele clade	<i>Echinometra oblonga</i> (n.a.)	E. sp. C (n.a.)	0.00
House mice				
Smadja & Ganem 2005	Mating preference	<i>Mus mus musculus</i> 7.50	<i>M. m. domesticus</i> 1.54	0.21
Other studies that do not include explicit information about both taxa, but that suggest asymmetrical displacement				
Hawaiian fruit flies				
Noor 1995	Mating preference	<i>Drosophila</i> spp.		
European Flycatchers				
Saetre et al. 1997	Mating preference	<i>Ficedula</i> spp.		
Spadefoot Toads				
Pfennig and Simovich 2002	Mating preference	<i>Spea</i> spp.		
Green-Eyed Tree Frogs				
Hoskin et al. 2005	Mating preference	<i>Litoria genimaculata</i>		
Chrysomelid Beetles				
Peterson et al. 2005	Mating preference	<i>Chrysochus</i> spp.		