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Character Displacement and the Origins of Diversity

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ABSTRACT: In *The Origin of Species*, Darwin proposed his principle of divergence of character (a process now termed “character displacement”) to explain how new species arise and why they differ from each other phenotypically. Darwin maintained that the origin of species and the evolution of differences between them is ultimately caused by divergent selection acting to minimize competitive interactions between initially similar individuals, populations, and species. Here, we examine the empirical support for the various claims that constitute Darwin’s principle, specifically that (1) competition promotes divergent trait evolution, (2) the strength of competitively mediated divergent selection increases with increasing phenotypic similarity between competitors, (3) divergence can occur within species, and (4) competitively mediated divergence can trigger speciation. We also explore aspects that Darwin failed to consider. In particular, we describe how (1) divergence can arise from selection acting to lessen reproductive interactions, (2) divergence is fueled by the intersection of character displacement and sexual selection, and (3) phenotypic plasticity may play a key role in promoting character displacement. Generally, character displacement is well supported empirically, and it remains a vital explanation for how new species arise and diversify.

Keywords: competition, Darwin’s divergence of character, hybridization, phenotypic plasticity, sexual selection, speciation.

Divergence of character ... is of high importance on my theory, and explains, as I believe, several important facts. (Darwin [1859] 2009, p. 111)

Natural selection, also, leads to divergence of character; for more living beings can be supported on the same area the more they diverge in structure, habits, and constitution, of which we see proof by looking at the inhabitants of any small spot or at naturalised productions. Therefore during the modification of the descendants of any one species, and during the incessant struggle of all species to increase in numbers, the more diversified these descendants become, the better will be their chance of succeeding in the battle of life. Thus the small differences distinguishing varieties of the same species, will steadily tend to increase till they come to equal the greater

differences between species of the same genus, or even of distinct genera. (Darwin [1859] 2009, pp. 127–128)

Introduction

With these words, Darwin first proposed that competition acts as a ubiquitous and powerful agent of divergent selection. Darwin’s ideas were groundbreaking, for none of his predecessors had viewed interactions among organisms as being significant in evolution (Ridley 2005). The crux of Darwin’s idea is that when organisms compete for scarce resources, natural selection should favor those individuals that are least like their competitors. Consequently, individuals, populations, and species that compete should become more dissimilar over time.

Darwin considered this process, which he dubbed “divergence of character,” to be of high importance for two reasons. First, it could explain the origin of species. According to Darwin, selection acting to minimize competition between “varieties” could drive divergence between them until they became separate species. Second, divergence of character could explain evolution’s distinctive treelike typology (reviewed in Ridley 2005). In particular, Darwin suggested that the divergent nature of evolution reflects the tendency for the strength of competition to increase with increasing taxonomic (and, hence, phenotypic) similarity between competitors. Darwin maintained that, “it is the most closely-allied forms,—varieties of the same species, and species of the same genus or related genera,—which, from having nearly the same structure, constitution and habits, generally come into the severest competition with each other. Consequently, each new variety or species, during the progress of its formation, will generally press hardest on its nearest kindred, and tend to exterminate them” (Darwin [1859] 2009, p. 110). Thus, by continually eliminating intermediate forms, competitively mediated selection has caused the history of life to resemble a tree, with numerous, diverging branches.

The concept of divergence of character was clearly important to Darwin’s thinking on the origin and diversity of species (reviewed in Mayr 1992; Tammone 1995; Ridley 2005; Costa 2009; Reznick 2010). Indeed, he devotes as much space in *The Origin of Species* to discussing it as he does to discussing natural selection. Yet, until relatively recently, evolutionary biologists questioned the role of

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competitive interactions in evolution (reviewed in Schluter 2000).

Here, we examine the empirical support for Darwin's ideas. We also discuss several key issues that Darwin failed to appreciate, which represent the focus of ongoing research. Specifically, we begin by describing how selection acting to lessen competitive interactions among organisms can lead to divergent trait evolution—a process now known as “character displacement” (Brown and Wilson 1956; Grant 1972; Schluter 2000, 2002). We also describe how this process of character displacement can trigger speciation. As we will see in the next section, Darwin's intuition was essentially correct: selection acting to minimize costly interactions between organisms can indeed promote divergent evolution and speciation. Yet, as we describe in the subsequent section, Darwin failed to appreciate the importance of divergence in reproductive characters, the effects of character displacement on sexual selection, and the importance of understanding the proximate mechanisms by which character displacement occurs. Nevertheless, Darwin's insights into the role of competition in divergence were well founded. Indeed, although character displacement was initially defined as the process of phenotypic divergence caused by interspecific resource competition (Brown and Wilson 1956), we now know that (as Darwin maintained and as we describe in greater detail below) an analogous process can arise from intraspecific competition. In short, character displacement, acting both between and within species, is well supported empirically, and it remains a compelling explanation for how new species arise and why they tend to be so different from each other phenotypically.

Before proceeding, it is important to note that there is some disagreement over what Darwin actually meant by “divergence of character.” Among those who equated divergence of character with character displacement (as we have) was Mayr (1963, 1970, 1992), who stated that, “The basic point of the principle of divergence is simplicity itself: the more the coinhabitants of an area differ from each other in their ecological requirements, the less they will compete with each other; therefore natural selection will tend to favor any variation toward greater divergence” (Mayr 1992, p. 344). By contrast, William Brown (who, with E. O. Wilson, coined the term “character displacement” [see Brown and Wilson 1956]) took issue with Mayr's interpretation and steadfastly maintained that the two terms were not synonymous, contending that “Darwin was describing what we call today *adaptive radiation*” (Brown 1964, p. 51). More recently, Tammone (1995) and Costa (2009) asserted that divergence of character does not describe a process in which divergence arises in sympatry. Instead, they argue that it describes the coming together of already divergent species that had previously

diverged in allopatry and were therefore able to coexist. Note, however, that this interpretation involves the sorting of species through differential extinction, which is not an evolutionary process (Schluter 2000).

While there is some ambiguity regarding what Darwin intended by “divergence of character,” Darwin's claims (from the quotes above) that “more living things can be supported on the same area the more they diverge” and that “each new variety or species ... will generally press hardest on its nearest kindred” suggest that he envisioned a process in which selection favored divergence between sympatric individuals that overlapped in ecological requirements. In other words, he seemed to be describing the process of character displacement (for further discussion, see Mayr 1970, 1992; Schluter 2001; Paterson 2005; Ridley 2005; Schemske 2010, in this issue).

What Darwin Got Right

In this section, we focus on the empirical support for Darwin's claims that (1) competition promotes divergent trait evolution, (2) the strength of competitively mediated divergent selection increases with increasing phenotypic similarity between competitors, (3) divergence can occur within species, and (4) competitively mediated divergence can trigger speciation. In our review, we emphasize studies of natural populations, especially those that combine observations with experiments. Generally, the most powerful method for demonstrating character displacement is to blend these two approaches (Schluter 2001, 2002).

Competition Promotes Divergent Trait Evolution

Darwin's central claim was that competition promotes divergent trait evolution. Yet he failed to provide any actual examples from natural populations. As it turns out, for Darwin to obtain such evidence would have been no trivial exercise; competitively mediated divergence is often difficult to detect. On the one hand, if two species are phenotypically similar enough to compete, they probably have not undergone much divergence. On the other hand, if two species have already undergone competitively mediated divergence, they are probably no longer similar enough to experience much competition with each other.

Lack (1947) was the first to resolve this conundrum. He introduced the method of comparing conspecific populations that are in sympatry with a heterospecific competitor versus those in allopatry. The logic behind this approach is as follows. Selection to lessen interspecific competition will act only in areas where species actually co-occur. Thus, if competition promotes divergence, species pairs should be more dissimilar where they occur together than where each occurs alone. In developing these ideas, Lack drew on de-

tailed studies of Darwin's finches from the Galápagos archipelago. He described several cases in which different finch species differed more in beak size where they were sympatric than where they were allopatric (Lack 1947).

Shortly after the appearance of Lack's seminal study, Brown and Wilson (1956) presented several additional cases in which species pairs were recognizably different in sympatry but not in allopatry. Their analysis therefore suggested that selection acting to lessen competitive interactions among organisms may often promote divergent trait evolution, a process they termed "character displacement" (Brown and Wilson 1956; see also Grant 1972; Schluter 2000, 2001, 2002). Following publication of that paper, researchers documented numerous instances of exaggerated divergence between sympatric species in diverse taxa (reviewed in Schluter 2000; Dayan and Simberloff 2005).

Despite mounting evidence of exaggerated divergence between sympatric species, some researchers remained skeptical of competition's role in generating such divergence (reviewed in Schluter 2001). The reason for such skepticism is that species may differ for evolutionary reasons other than selection and for selective reasons other than to avoid competition (Grant 1972; Arthur 1982; Losos 1992; Schluter and McPhail 1992; Taper and Case 1992; Marko 2005). Thus, a major challenge for researchers in the field of character displacement has been to rule out other causes of species divergence that could produce the same patterns as character displacement. One approach for doing so is to establish rigorous criteria that when met would make a compelling case for character displacement (Grant 1972; Arthur 1982; Schluter and McPhail 1992; Taper and Case 1992; Losos 2000). A number of studies have applied such criteria to make a strong case for character displacement (e.g., see Schluter and McPhail 1992; Adams and Rohlf 2000; Caruso 2000). Moreover, documenting parallel evolution in resource acquisition traits—specifically, establishing that a divergent trait has evolved repeatedly in closely related, independently evolving populations—implicates competitively mediated selection as the cause of trait divergence between species (e.g., see Schluter and McPhail 1992; Hansen et al. 2000; Matocq and Murphy 2007; Rice et al. 2009; Adams 2010).

A second approach for making a compelling case for character displacement is to utilize experiments. The ideal experimental demonstration of character displacement would be to manipulate the presence of a competitor and show that characters associated with resource use evolve in a focal species. However, such experiments are generally not attempted except in lab populations with short generation times (see Tyerman et al. 2008). Nevertheless, "natural experiments" suggest that character displacement can be observed directly in the wild. For example, in long-term field studies of Darwin's finches, Grant and Grant

(2006) established that the medium ground finch *Geospiza fortis* diverged in beak size from the large ground finch *Geospiza magnirostris* after the latter species invaded the former species' island and became numerous enough to deplete the food supply (fig. 1).

Many species are also amenable to experiments aimed at testing key predictions of Darwin's hypothesis. Two classes of such experiments have been used. One class observes the performance of a focal species after manipulating the presence (or relative abundance) of a heterospecific competitor (Schluter 1994; Pfennig et al. 2007). A second class of experiments uses species that respond to competitors through phenotypic plasticity (Pfennig and Murphy 2000, 2002). With such species, a causal link can be established between the presence of competitors and character change if, in the presence of a competitor, an individual facultatively expresses an alternative resource-use phenotype distinct from that of its competitor (fig. 2). The case for character displacement is especially persuasive if these experimentally demonstrated phenotypic shifts mirror divergence in these same traits observed between natural populations in sympatry versus allopatry with a competitor (e.g., see fig. 2). In sum, although resource competition is not the only agent of divergent selection, the available data suggest that resource competition can indeed promote divergent trait evolution, as Darwin initially proposed.

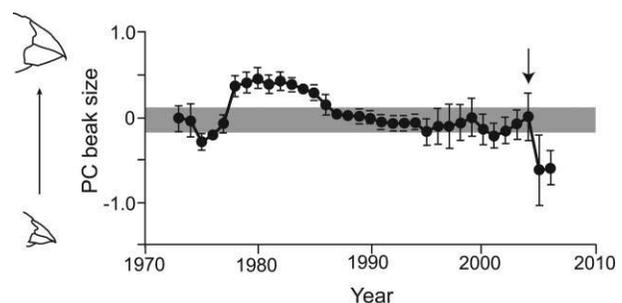


Figure 1: Direct evidence of character displacement in medium ground finches, *Geospiza fortis*, as revealed by changes in beak size (measured as a principal component score, *PC*). Shown is the mean beak size ($\pm 95\%$ confidence intervals) for a population of *G. fortis* on an undisturbed Galápagos island. In 1982, the large ground finch *Geospiza magnirostris* arrived on the island and began to compete with the resident population of *G. fortis* for seeds, especially in the dry season when food is limiting. By the time a severe drought struck in 2003, the population size of *G. magnirostris* had increased substantially. Character displacement in *G. fortis* occurred in 2004–2005 (arrow), when selection acting against large-beaked *G. fortis* led to the evolution of greatly reduced beak size among *G. fortis*. Gray bar marks the 95% confidence limits on the estimate of the mean in 1973 to illustrate subsequent changes in the mean. Redrawn from Grant and Grant (2006).

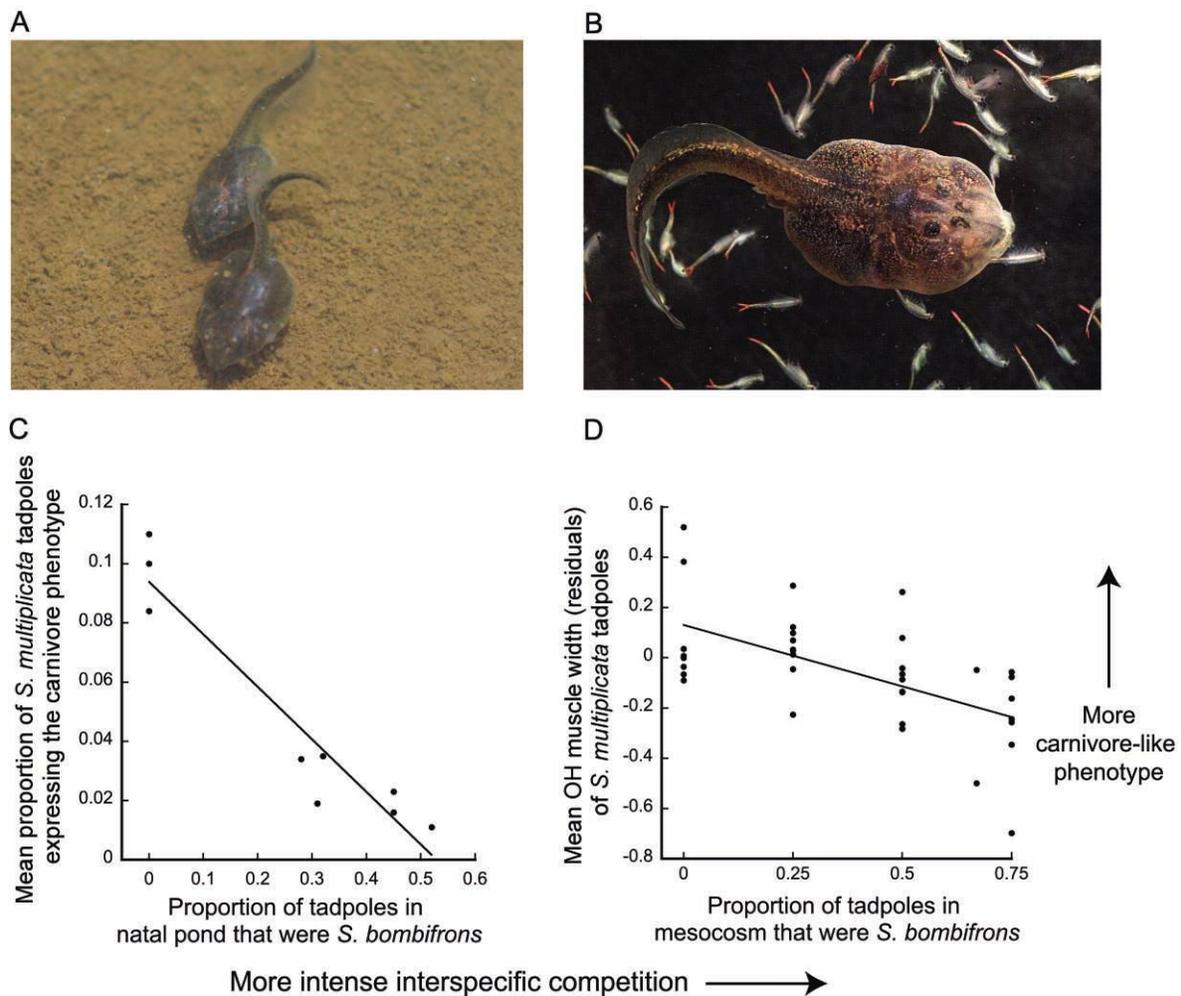


Figure 2: Experimental evidence of character displacement in Mexican spadefoot toad tadpoles *Spea multiplicata*. *Spea* tadpoles occur as an omnivore ecomorph (A), which feeds on detritus on the pond bottom, and a morphologically distinctive carnivore ecomorph (B), which feeds on and whose phenotype is induced by anostracan fairy shrimp (shown surrounding the tadpole). Plains spadefoot toad tadpoles *Spea bombifrons*, which are similar in morphology and diet, outcompete *S. multiplicata* for shrimp. C, Presumably because of selection imposed by *S. bombifrons*, *S. multiplicata* have undergone character displacement in tadpole morph production, but the degree of this character displacement increases with increasing intensity of interspecific competition: *S. multiplicata* tadpoles whose parents were derived from populations that historically have had more contact with *S. bombifrons* possess the lowest propensities to produce carnivores, even when tadpoles from different populations are reared under common conditions, suggesting that these population differences in morph expression are canalized. D, In contrast to the situation in sympatry, *S. multiplicata* derived from allopatry possess plasticity to produce both ecomorphs. Thus, these individuals can be used to experimentally evaluate whether the presence of *S. bombifrons* per se has likely caused the canalized differences in tadpole morph production observed between sympatric populations and illustrated in C. Such experiments reveal that allopatric *S. multiplicata* tadpoles produce increasingly fewer carnivore-like tadpoles (as indicated by the size of their orbitohyoideus muscle, OH) as the frequency of *S. bombifrons* is experimentally increased, mirroring the canalized shifts observed in natural populations in C. Data in C from Pfennig and Murphy (2002) and Martin and Pfennig (2010); data in D from Pfennig and Murphy (2002).

The Strength of Competitively Mediated Divergent Selection Increases with Increasing Phenotypic Similarity between Competitors

Darwin did not envision competitively mediated divergence as transpiring with equal likelihood or degree between all organisms. Instead, he argued that “it is the most

closely-allied forms,—varieties of the same species, and species of the same genus or related genera,—which, from having nearly the same structure, constitution and habits, generally come into the severest competition with each other” (Darwin [1859] 2009, p. 110). Thus, according to Darwin, competition is the most severe between those individuals that are the most closely related to each other,

because such individuals should be most similar in resource use and in associated traits. This claim was central to Darwin's arguments for explaining, among other things, why evolution, on the grand scale, has a treelike structure (see "Introduction"). This claim is also vital for ecology in that it forms the basis for the competitive exclusion principle (Hardin 1960), which states that species with similar resource requirements cannot stably coexist. The competitive exclusion principle was elegantly demonstrated by Gause's (1934) pioneering experiments with *Paramecium*. But is there any evidence to suggest, as Darwin maintained, that the strength of competitively mediated divergent selection increases the more similar two species are to each other in resource use?

Experiments have shown that during character displacement natural selection disfavors individuals that express resource-use phenotypes most closely resembling those of their heterospecific competitor (e.g., see fig. 3; see also Pacala and Roughgarden 1985; Pritchard and Schluter 2001; Gray and Robinson 2002; Schluter 2003). Thus, as predicted by Darwin, the strength of divergent selection on resource-use traits increases the more similar two species are to each other in resource use.

A number of researchers have also evaluated Darwin's claim by using phylogenetic distance as a proxy for similarity in resource use. The underlying assumption behind this alternative approach is that there should be a negative relationship between the phylogenetic distance of any two species and their overall ecological similarity (e.g., see Webb et al. 2002; Losos 2008). Although phylogenetic distance does not always predict ecological similarity (Losos 2008), phylogenetically close taxa might be more likely to compete if the fundamental niche is conserved evolutionarily (Maherali and Klironomos 2007). Indeed, there is evidence that communities are more species rich when they consist of phylogenetically distinct taxa that are less likely to overlap in resource use and, hence, compete with each other (Maherali and Klironomos 2007). Moreover, communities may often consist of species that are more phylogenetically dissimilar than would be expected by chance (e.g., Cavender-Bares et al. 2004; but see Webb 2000; note, however, that we would not expect communities to be phylogenetically overdispersed if competing species within these communities undergo character displacement rather than competitive exclusion).

Thus, ample empirical evidence exists to support Darwin's claim that the intensity of divergent selection increases the more similar two species are to each other ecologically, phenotypically, and (possibly) even phylogenetically. However, our discussion has focused so far on how the strength of competitively mediated divergent selection increases with increasing ecological similarity between heterospecific competitors. Yet, the most ecologi-

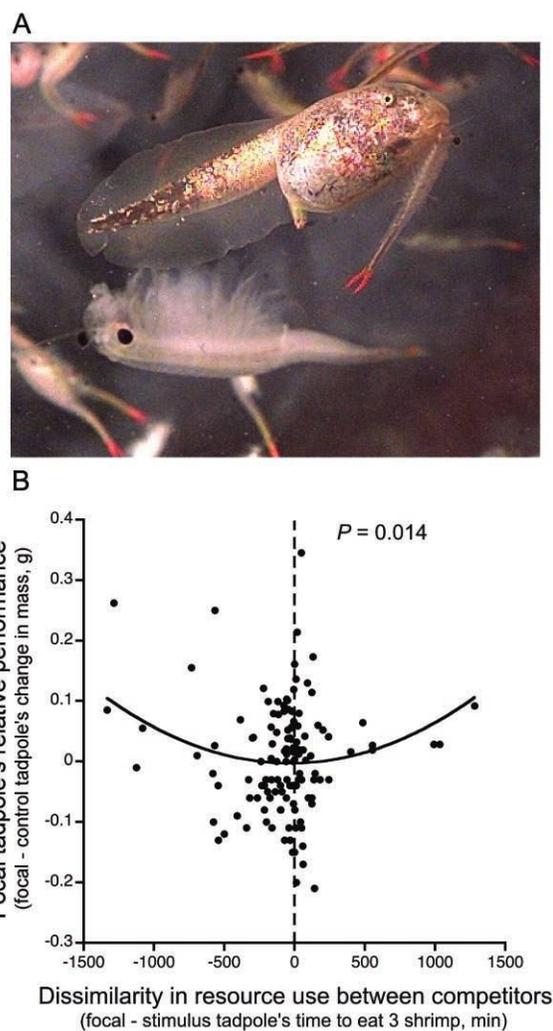


Figure 3: Experimental evidence that divergent natural selection disfavors those individuals that are the most similar to their competitor in resource use. *A*, Mexican spadefoot toad tadpoles, *Spea multiplicata*, compete with a heterospecific, *Spea bombifrons*, for anostracan fairy shrimp, which are often limited in natural ponds. Within natural populations of both species, individuals typically vary in their inherent propensity to eat shrimp. *B*, When individual *S. multiplicata* tadpoles are housed with a single *S. bombifrons* tadpole, the more similar the two individuals are, the lower the growth of the focal *S. multiplicata* tadpole (regardless of which species ate shrimp faster). The curved line is a quadratic regression estimate of relative growth (a proxy for fitness) as a function of a focal *S. multiplicata* tadpole's similarity in resource use to its *S. bombifrons* competitor, as measured by the time it took each individual to consume shrimp prey. Redrawn from Pfennig et al. (2007).

cally similar competitors that most organisms will confront are likely to be conspecifics, and Darwin clearly thought that competitively mediated divergence could also occur within species (see quote above). Indeed, compared to interspecific competition, intraspecific competition is

probably more common and often stronger (Gurevitch et al. 1992). In particular, intraspecific competition is probably more common, because individuals likely encounter conspecifics more frequently than heterospecifics. Moreover, intraspecific competition is probably often stronger than interspecific competition because conspecifics are typically more similar in resource-use requirements than are heterospecifics, thereby making interactants more evenly matched and competition more intense (see above). Given that intraspecific competition is common and frequently strong, can selection lessen such competition by promoting divergence within species through “intraspecific character displacement” (sensu West-Eberhard 2003; see also Dayan and Simberloff 2005)?

Divergence Can Occur within Species

Darwin maintained that competition promotes divergence within species. As we noted in the “Introduction,” selection acting to reduce such intraspecific competition can promote divergence within species through a process that is the intraspecific analog to interspecific character displacement (Dayan and Simberloff 2005; Pfennig and Pfennig 2009). Here, we describe how intraspecific character displacement can and does arise.

A common manifestation of intraspecific character displacement is niche width expansion (Huxley [1942] 2010; Van Valen 1965; MacArthur and Wilson 1967; Roughgarden 1972). An increase in niche width is frequently observed in populations on isolated archipelagos or similar islandlike settings (e.g., lakes), where individuals encounter few heterospecific competitors (MacArthur and Wilson 1967). In such situations, populations are free to respond adaptively to intraspecific competition by expanding their niche width to take advantage of underexploited resources (a process termed “ecological release” or “character release”; Wilson 1961; Grant 1972; for empirical examples, see Werner and Sherry 1987; Robinson and Wilson 1994; Simberloff et al. 2000).

Roughgarden (1972) described how this process could arise. Consider a hypothetical population that exploits a continuously varying resource gradient, such as a gradient of prey size. If all resource types along the gradient (e.g., all prey size classes) are not utilized to the same extent, then those individuals that specialize on underutilized portions of the resource-use gradient (e.g., size classes that are underutilized) should experience less intense intraspecific competition (Roughgarden 1972). Essentially, individuals experiencing intraspecific competition are expected to equalize the level of competition by spreading themselves out more or less evenly along the resource-use gradient (MacArthur 1972), assuming that such ecological opportunity is available to them (Simpson 1953). This

process can drive a population onto a novel resource for which competition is less severe (Bolnick 2001) and thereby possibly promote the evolution of novel resource-use phenotypes (e.g., see Carroll et al. 1998; Jones 1998; Aubret et al. 2006; Herrel et al. 2008). By favoring novel resource-use phenotypes, intraspecific character displacement might even trigger adaptive radiation (Simpson 1953; Schluter 2000).

Another common manifestation of intraspecific character displacement—and one that can have important ramifications—is the evolution of discrete phenotypes within populations (i.e., polymorphism; Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2003). Intraspecific competition has long been viewed as a key agent of disruptive selection (Rosenzweig 1978; Wilson and Turelli 1986; Day and Young 2004; Rueffler et al. 2006), which arises when extreme phenotypes have a fitness advantage over more intermediate phenotypes (Mather 1953). Dieckmann and Doebeli (1999) and Doebeli and Dieckmann (2003) described how this process could unfold. Consider a population that exploits a continuously varying resource gradient, such as a gradient of prey sizes, where prey of intermediate size are most common. Individuals that specialize on the intermediate resource type (e.g., prey of intermediate size) should start out with a fitness advantage, because the intermediate resource type is most frequently encountered. Over time, however, the intermediate resource type should become increasingly depleted, and individuals specializing on this resource should cease to be favored. Instead, individuals with extreme resource-use traits that specialize on less common resources on either end of the resource gradient (e.g., very small or very large prey) will have a fitness advantage (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2003). This process is ultimately driven by negative frequency-dependent selection, in which rare resource-use phenotypes have a fitness advantage because of decreased competition with more common phenotypes (Day and Young 2004; Rueffler et al. 2006). If such selection persists, it could promote the evolution of a resource polymorphism—the occurrence within a single population of discrete intraspecific morphs showing differential resource use (Smith and Skúlason 1996; see table 1).

Historically, disruptive selection was thought to be rare (Endler 1986). Yet disruptive selection may be more widespread in nature than was formerly presumed (Kingsolver et al. 2001). Indeed, recent field research has uncovered evidence of both disruptive selection acting on resource-acquisition traits (Smith 1993; Medel et al. 2003; Bolnick 2004; Pfennig et al. 2007; Bolnick and Lau 2008; Calsbeek and Smith 2008; Hendry et al. 2009; Martin and Pfennig 2009) and frequency-dependent intraspecific competition for resources, such that individuals compete most against

Table 1: Resource polymorphisms in selected taxa showing the nature of the ecological differences between alternative resource-use ecomorphs

Organism	Nature of ecological differences	Reference
Viruses:		
Lambda bacteriophage	Lysis vs. lysogeny reproduction	Ptashne 1986
Ciliates:		
<i>Tetrahymena vorax</i>	Bacterivore vs. carnivore niches	Ryals et al. 2002
<i>Lembadion bullinum</i>	Noncannibal vs. cannibal niches	Kopp and Tollrian 2003
Rotifers:		
<i>Asplanchna sieboldi</i>	Noncannibal vs. cannibal niches	Gilbert 1973
Insects:		
Blueberry and apple maggot flies ^a	Different host plants	Feder et al. 1989
Leaf beetles ^a	Different host plants	Funk 1998
Goldenrod ball gallmakers ^a	Different host plants	Abrahamson et al. 2001
Walking sticks ^a	Different host plants	Nosil et al. 2002
Fish:		
Sunfish	Benthic vs. limnetic niches	Robinson et al. 1993
Numerous Nearctic freshwater fish	Benthic vs. limnetic niches	Robinson and Wilson 1994
Sockeye salmon ^a	Different habitat preferences	Hendry et al. 2000
Three-spine sticklebacks ^a	Benthic vs. limnetic niches	Rundle et al. 2000
Lake Nicaragua cichlids ^a	Benthic vs. limnetic niches	Barluenga et al. 2006
Amphibians:		
Tiger salamander larvae	Planktivore vs. cannibal niches	Collins and Cheek 1983
Tiger salamander larvae	Paedomorph vs. metamorph life histories	Collins 1981
Spadefoot toad tadpoles ^a	Omnivore vs. carnivore niches	Rice and Pfennig 2010
Birds:		
Seedcracker finches	Different food niches	Smith 1993
Crossbills ^a	Different food niches	Smith and Benkman 2007
Darwin's finches ^a	Different food niches	Huber et al. 2007

^a Natural populations that differ in morph expression are (potentially) partially reproductively isolated from each other.

conspecifics bearing similar resource-use phenotypes (Pfennig 1992; Hori 1993; Benkman 1996; Maret and Collins 1997; Martin and Pfennig 2009). Thus, intraspecific character displacement—trait evolution stemming from selection to lessen intraspecific competition—might often promote divergence within species, as Darwin suggested.

Competitively Mediated Divergence Can Trigger Speciation

Darwin ([1859] 2009) first suggested that speciation could arise when individuals in a population began to diverge from one another as a result of selection to lessen competitive interactions (see quote in the “Introduction”). As with the previous claim, Darwin's contention that competitively mediated divergence could lead to speciation initially met with opposition. In particular, Darwin's emphasis on ecological differentiation within contiguous populations as a cause of speciation was first challenged by Moritz Wagner, George Romanes, John Gulick, and others who maintained that divergent evolution cannot occur without some sort of geographical isolation (Tammone 1995). Later, Mayr (1963) argued that the nonallopatric speciation implied by Darwin's model is implau-

sible, because gene flow would preclude divergence. In fact, as a mechanism for explaining the origin of species, Mayr (1992, p. 358) concluded that “it is now evident that the principle of divergence is invalid.” However, while it is true that Darwin erred in “not discriminating between intrapopulation variants and geographic subspecies, calling both of them varieties” and in “his failure to distinguish between isolation in an ecological niche and in a geographically isolated area” (Mayr 1992, p. 358), Darwin did highlight how competitive interactions could promote the formation of species. Furthermore, recent theory and data demonstrate that substantial divergence and even speciation can occur in the face of gene flow (Kirkpatrick and Ravigne 2002; Bush and Butlin 2004; Dieckmann et al. 2004; Bolnick and Fitzpatrick 2007; Nosil 2008; Sobel et al. 2010). Indeed, the notion that competitively mediated divergence can lead to speciation—even within a continuous population—is now seen as plausible (Dieckmann and Doebeli 1999; Polechová and Barton 2005).

Here, we review three evolutionary routes by which character displacement might promote speciation. The first two routes are noncontroversial. In these two routes, speciation proceeds either following secondary contact be-

tween previously divergent populations (the first route) or when populations that are (potentially) parapatric diverge (the second route). Only the third route involves the controversial notion that ecological differentiation within a contiguous population can result in speciation.

First, competitively mediated divergence might finalize the process of speciation. This scenario entails the classical allopatric model of speciation (Mayr 1963; Coyne and Orr 2004). Speciation begins when populations in allopatry start to diverge from one another (e.g., due to divergent selection or genetic drift). When such populations come into secondary contact, selection to minimize competition can accentuate divergence between them (Coyne and Orr 2004; Grant and Grant 2008; Price 2008). Moreover, if these incipient species interbreed and produce hybrids of low fitness, then reinforcement can finalize speciation by promoting the evolution of complete reproductive isolation (Dobzhansky 1940; Howard 1993; Servedio and Noor 2003; Coyne and Orr 2004). For possible examples, see reviews by Coyne and Orr (2004), Grant and Grant (2008), and Schluter (2009).

Second, competitively mediated divergence might initiate the evolution of reproductive isolation between (potentially parapatric) populations that differ in interactions with heterospecifics (Pfennig and Pfennig 2009; Rice and Pfennig 2010). Because individuals in sympatry with a heterospecific competitor will experience a different selective environment from conspecifics in allopatry, populations in these two types of environments should also diverge. Such divergence may indirectly promote speciation through the evolution of either postmating or premating barriers to gene flow between sympatric and allopatric populations. Postmating barriers may arise when offspring created by matings between sympatric and allopatric parents express an intermediate phenotype that is not well adapted for either parental environment (Rice and Hostert 1993; Hatfield and Schluter 1996, 1999; Pfennig and Rice 2007; Svedin et al. 2008). Such divergence would be further exaggerated if populations evolving independently of each other in divergent competitive environments accumulated alleles that were incompatible with genomes from the alternative environment (Coyne and Orr 2004). Moreover, as we describe in more detail below, premating barriers may arise if shifts in habitat or resource use preclude mating between individuals from alternative competitive environments (reviewed in Rundle and Schluter 2004).

Third, competitively mediated divergence might promote sympatric speciation by favoring the evolution of resource polymorphism (table 1). As noted above, this route is more controversial than the first two routes, because divergence occurs among potentially interbreeding individuals (i.e., within sympatric populations). However,

the evolution of a resource polymorphism has long been viewed as a critical early stage of the speciation process (Huxley [1942] 2010; Maynard Smith 1966; Felsenstein 1981; West-Eberhard 1989, 2003, 2005; Meyer 1993; Wimberger 1994; Smith and Skúlason 1996; Skúlason et al. 1999; Stauffer and Gray 2004; Mallet 2008; Elmer et al. 2010). This view is based partly on the observation that the phenotypic differences between alternative morphs are often comparable to those normally seen between species within the same clade (e.g., see Liem and Kaufman 1984; Hendry et al. 2006; Calsbeek et al. 2007). Moreover, populations that differ in expression of resource polymorphism typically possess some of the same characteristics as species, including ecological and genetic differences and even partial reproductive isolation (see table 1), suggesting the presence of incipient species (West-Eberhard 2005; Mallet 2008; Hendry 2009).

The evolution of resource polymorphism might be particularly effective at facilitating speciation, because the same conditions that promote resource polymorphism simultaneously foster speciation's three components—genetic isolation, divergence, and reproductive isolation (Pfennig and McGee 2010). Genetic isolation can arise between morphs, because alternative resource-use morphs typically differ in the locations and times that they seek their separate resources (e.g., see Robinson and Wilson 1994; Wimberger 1994; Skúlason et al. 1999; Robinson and Parsons 2002; Nosil 2007) and thereby, potentially, where and when they seek mates (especially in phytophagous insects, where different host races [a form of resource polymorphism] mate on their host [Berlocher and Feder 2002; Bush and Butlin 2004]).

Such isolation between ecomorphs can thereby enable natural selection to further enhance existing differences between the alternative morphs (and also between populations that differ in the expression of such morphs). In particular, natural selection will generally favor morph-specific traits that improve a morph's ability to exploit its particular niche (e.g., see Schluter 1993; Nosil 2007; Sobel et al. 2010). Moreover, as we describe in more detail below, even small-scale ecological separation can influence patterns of sexual selection, which could further enhance divergence between morphs (Boughman 2001).

Once alternative morphs begin to accumulate these ecological and genetic differences, matings between them should produce offspring with low fitness (Hatfield and Schluter 1999). Consequently, selection will favor the evolution of further reproductive isolation between ecomorphs (Nosil et al. 2002; Rundle and Schluter 2004). Moreover, matings between populations that differ in the expression of these phenotypic alternatives should also produce offspring of low fitness (Pfennig and Rice 2007). Ultimately, selection should favor the evolution of repro-

ductive isolation between ecomorphs and also between populations expressing different frequencies of ecomorphs (Rice and Pfennig 2010), thereby completing speciation.

As evidence of resource polymorphism's possible role in speciation, clades in which resource polymorphism has evolved are more species rich than their sister clades that lack resource polymorphism (Pfennig and McGee 2010). More direct tests are needed, however. Organisms with short generation times that shift hosts and mate on their host, such as certain microbes (Duffy et al. 2007) and phytophagous insects (Berlocher and Feder 2002; Bush and Butlin 2004), might prove especially useful for evaluating competition's role in sympatric divergence and speciation. In sum, competitively mediated divergence might play a critical role in promoting speciation, including between groups of organisms in a contiguous population.

What Darwin Failed to Appreciate

Having reviewed what Darwin got right regarding competition's role in diversification, we now highlight those aspects of character displacement that he failed to appreciate. Specifically, we describe how (1) divergence can arise from selection acting to lessen reproductive interactions, (2) divergence is fueled by the intersection of character displacement and sexual selection, and (3) phenotypic plasticity might play a key role in promoting character displacement.

Divergence Can Arise from Selection Acting to Lessen Reproductive Interactions

Darwin's principle of divergence of character was predicated on the notion that selection to lessen competition for resources is the primary driver of diversification. By contrast, he failed to appreciate that selection could act similarly to lessen reproductive interactions (fig. 4) and that such selection could generate divergence rivaling that generated by resource competition (Lack 1945; Brown and Wilson 1956).

When sharing the environment for reproduction, heterospecifics can interact directly or indirectly (reviewed in Pfennig and Pfennig 2009). During direct interactions, individuals actually risk mating with heterospecifics. During indirect interactions, heterospecifics compete for access to the locations, signaling space, or means that allow for mate localization and attraction (Butlin and Ritchie 1994). Both types of interactions can exert strong selection on the evolution of the timing and nature of reproduction so as to minimize costly reproductive interactions with heterospecifics. Ultimately, this selection can cause species to diverge from one another in reproductive traits (a process known as "reproductive character displacement"; Brown

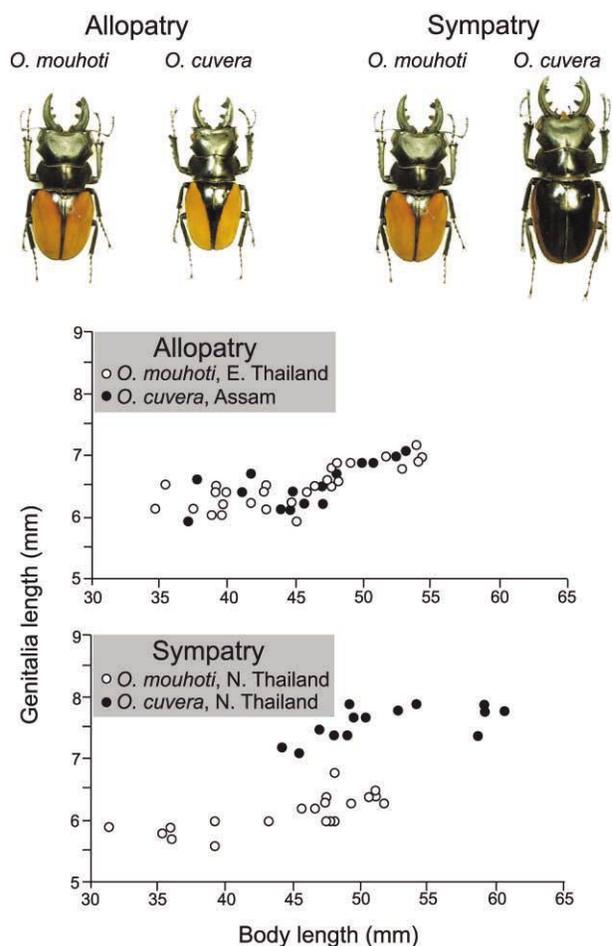


Figure 4: Evidence of reproductive character displacement, as revealed by exaggerated divergence in sympatry between two species of stag beetles from Southeast Asia (genus *Odontolabis*). In allopatry, *Odontolabis mouhoti* and *Odontolabis cuvera* are similar in body size, genitalia length, and coloration. In sympatry, these two species show exaggerated divergence in these characters, all of which have been implicated in mate acquisition. Beetles redrawn from Kawano (2003), and data from Kawano (2003).

and Wilson 1956; Crozier 1974; reviewed in Howard 1993; Andersson 1994; Butlin and Ritchie 1994; Gerhardt and Huber 2002; see also Groning and Hochkirch 2008; Pfennig and Pfennig 2009).

Whether via direct or indirect interactions, selection to avoid reproductive interactions with heterospecifics results in "reproductive partitioning" of both the environment and trait space. In terms of partitioning of the environment, different species may use different locations or times for their reproductive activities (e.g., Ptacek 1992). In terms of trait space, males may adopt sexual signals that are more distinct from those of heterospecifics, whereas females may adopt mating preferences or evolve sensory filters that enhance the likelihood of mating with conspe-

cifics (reviewed in Howard 1993; Andersson 1994; Butlin and Ritchie 1994; Gerhardt and Huber 2002). Moreover, females may evolve reproductive strategies that prevent hybrid zygote production, such as conspecific sperm precedence or reduced investment in, or production of, offspring resulting from heterospecific matings (reviewed in Howard 1999). In the absence of such reproductive partitioning, species may coalesce via hybridization (e.g., Seehausen et al. 1997; Behm et al. 2010) or one may become extinct via reproductive exclusion (Hochkirch et al. 2007; Groning and Hochkirch 2008).

Divergence in reproductive traits is not divorced from divergence in ecological traits (Rice and Hostert 1993; Ryan 1998; Boughman 2002; Podos and Nowicki 2004; Grant and Grant 2008; Price 2008; Pfennig and Pfennig 2009; Sobel et al. 2010). Indeed, divergence in ecological traits is unlikely to occur without also potentially altering both male and female traits involved in reproduction (e.g., Boughman 2001; Podos 2001). For example, selection to minimize competition for resources among different species of Darwin's finches has led to divergence in resource use and, consequently, changes in beak size and morphology (e.g., see fig. 1). These changes in beak size and morphology are associated with a concomitant shift in the male's song, which is directly involved in species recognition (reviewed in Podos and Nowicki 2004; Grant and Grant 2008; Price 2008). Indeed, within the finch *Geospiza fortis*, two morphs have evolved that are specialized for using alternative seed sizes (Hendry et al. 2006, 2009). Their songs appear to have diverged in concert with changes in beak size, and this shift has resulted in assortative mating based on song type and, therefore, beak size (Huber and Podos 2006; Huber et al. 2007).

Divergence in ecological traits might also alter female mate preferences (reviewed in Ryan 1998; Boughman 2002; Pfennig and Pfennig 2009; Sobel et al. 2010). Consequently, such divergence in female mate preferences might minimize reproductive interactions between divergent populations and thereby initiate the evolution of reproductive isolation (e.g., Boughman 2001; reviewed in Boughman 2002; Pfennig and Pfennig 2009). For example, certain stickleback populations have diverged into two sympatric ecomorphs in response to selection to lessen resource competition: benthics, which forage in the littoral zone, and limnetics, which forage in open water (reviewed in Rundle and Schluter 2004). These two ecomorphs have diverged not only in resource use but also in female mate preferences. In particular, whereas red coloration is more difficult to detect in the littoral zone, it is more easily discerned in open water (Boughman 2001). Consequently, benthic females are less sensitive to variation in red than are limnetic females, and unlike limnetic females, benthic females do not tend to prefer redder males (Boughman

2001, 2007). Moreover, males are redder in populations where females can detect and prefer redder males (Boughman 2001, 2007). Perhaps more critically, the two ecomorphs within any given lake are, at least partly, reproductively isolated from each other (reviewed in Rundle and Schluter 2004). The extent to which populations are isolated is negatively correlated with the difference in female red sensitivity and preference between populations. Thus, shifts in mate preference—tied to divergent selective environments—dictates the degree to which reproductive divergence has occurred (Boughman 2001).

Is such divergence in reproductive traits a by-product of shifts in habitat associated with resource use, or have reproductive traits become targets of selection to minimize reproductive interactions between ecomorphs or species? In sticklebacks, divergence in reproductive characters does not appear to be an artifact: in a study that specifically controlled for the effects of divergence in resource use, sympatric limnetics and benthics displayed enhanced reproductive isolation relative to allopatric pairs (Rundle and Schluter 1998, 2004). Presumably, ecological divergence generated differences in traits used during mating that then became further elaborated to avoid the costs of mating with heterospecifics (Rundle and Schluter 1998, 2004; Boughman et al. 2005).

Although recent studies have focused on how divergence in ecological traits can affect divergence in reproductive traits, the reverse could also hold. In other words, divergence in reproductive traits could drive divergence in ecological characters (Konuma and Chiba 2007). If, for example, species segregate in space or time to avoid reproductive interactions, they may be concomitantly exposed to novel, underutilized resources. If utilization of these resources is selectively favored to minimize resource competition between species, then divergence in reproductive traits can instigate divergence in resource use (Konuma and Chiba 2007).

That both ecological and reproductive characters can diverge in concert has two important outcomes for diversity. First, divergence of resource-use traits in tandem with reproductive traits potentially stabilizes the evolution of divergent ecological traits (i.e., it explains how alternative morphs can persist). In the absence of reproductive divergence, different species or different ecomorphs might interbreed, and any ecological specialization that each species/ecomorph has started to evolve might break down as a consequence of genetic mixing between the two divergent groups (e.g., Seehausen et al. 1997; Behm et al. 2010). If, however, reproductive characters diverge in concert with ecological traits, interbreeding is less likely to occur, and specialized forms can be maintained and elaborated as we described above (e.g., Huber and Podos 2006; Huber et al. 2007).

A second significant outcome of the divergence of reproductive characters in conjunction with ecological specialization is enhanced reproductive isolation between existing species, or alternatively, speciation between alternative ecomorphs (Rice and Hostert 1993; Boughman 2002; Coyne and Orr 2004; Podos and Nowicki 2004; Rundle and Nosil 2005; Grant and Grant 2008; Price 2008; Pfennig and Pfennig 2009; Sobel et al. 2010). In particular, because differential reproductive behaviors are linked to alternative resource-use types, the likelihood of assortative mating within type is higher than it would be if these different types of traits were unlinked. Such assortative mating enhances the evolution of reproductive isolation and potentially increases the likelihood of speciation relative to situations where the traits are disassociated (Rice and Hostert 1993; Bolnick and Fitzpatrick 2007).

Moreover, as each species (or ecomorph) becomes increasingly specialized, the detrimental fitness consequences of hybridization can become exaggerated, because hybrids (1) will not succeed in either parent's niche, (2) cannot attract or identify mates, and/or (3) might suffer from genetic incompatibilities that arise between the alternate genomes (see above). Consequently, this selection against hybrids favors further reproductive divergence, which may ultimately contribute to reproductive isolation—and complete speciation—between competing species or ecomorphs (Coyne and Orr 2004; Rundle and Nosil 2005; Grant and Grant 2008; Price 2008; Ortiz-Barrientos et al. 2009; Pfennig and Pfennig 2009; Schluter 2009; Sobel et al. 2010). Reproductive character displacement thereby serves as a critical link between divergence in resource use and the origin of species.

Divergence Is Fueled by the Intersection of Character Displacement and Sexual Selection

Darwin's lack of focus on reproductive interactions driving divergence is ironic, because it was he who first proposed sexual selection as a mechanism for the adaptive evolution of sexual traits (Darwin [1859] 2009). Darwin mentions sexual selection in *The Origin of Species* as arising from interactions within species, specifically competition among males for access to females. Yet he regarded sexual selection as "less rigid in its action than ordinary selection" (Darwin [1859] 2009, p. 157). Perhaps even more importantly, he failed to describe why species differ in sexually selected traits. Indeed, we still do not fully understand why species and populations differ in patterns of sexual selection. Variation in patterns of sexual selection could arise simply by chance (Lande 1981; Kirkpatrick 1982). Alternatively, differential experience with abiotic factors (e.g., the physical conditions through which signals are transmitted) and biotic factors (e.g., predators) could alter the nature and

targets of selection on reproductive traits (reviewed in Endler and Basolo 1998; Pfennig 1998; Ryan 1998; Ptacek 2000; Boughman 2002; Price 2008). Here, we focus on how resource competition or reproductive interactions can influence the nature of sexual selection and thereby generate adaptive variation in patterns of sexual selection that possibly even promotes speciation.

As indicated above, character displacement in both ecological and reproductive traits will tend to alter sexual signals, mate preferences, and the habitat in which they are expressed. Such changes will not only minimize reproductive interactions and resource competition between species but will also alter mate choice and male-male interactions within species (e.g., Pfennig 2000; Boughman 2007; Higgie and Blows 2007). Character displacement thereby alters the targets of sexual selection within species and the selective context in which sexual signals are expressed and perceived. In doing so, competitive and reproductive interactions between species can cause patterns of sexual selection to vary between them (reviewed in Pfennig 1998; Ryan 1998; Ptacek 2000; Boughman 2002; Price 2008; Ortiz-Barrientos et al. 2009; Pfennig and Pfennig 2009; Sobel et al. 2010).

Character displacement can also have important effects on the underlying fitness consequences of sexual selection. Consider, for example, that sexual selection theory generally predicts that females should prefer exaggerated traits because these indicate male quality (reviewed in Andersson 1994). If, however, heterospecifics possess elaborate traits, selection may promote the evolution of preferences for less exaggerated signals that are most dissimilar from those of heterospecifics (Ryan and Rand 1993; Pfennig 1998). Yet, by adopting such preferences to avoid costly heterospecific interactions, females may concomitantly forgo information about a prospective conspecific mate's ability to convey additional fitness benefits (Pfennig 2000, 2008; Higgie and Blows 2007, 2008).

The resulting fitness trade-offs (i.e., avoiding the costs of heterospecific interactions at the loss of benefits of high-quality matings) can explain why divergent mating traits that evolve in sympatry do not spread back into allopatry via gene flow (Pfennig and Pfennig 2005; Higgie and Blows 2007). Indeed, when trade-offs in mate choice arise, sympatric and allopatric populations can experience nearly opposing patterns of mate-choice-mediated sexual selection. Consequently, not only will mate preferences diverge between sympatry and allopatry but sexual signals (and any correlated traits) will also diverge (Pfennig and Pfennig 2005; Higgie and Blows 2007, 2008).

Because divergence between species contributes to divergence within species between sympatric and allopatric populations, resource competition and reproductive interactions between species can lead to different patterns

of sexual selection in different conspecific populations (Pfennig 1998; Ptacek 2000; Boughman 2002; Pfennig and Ryan 2007; Price 2008; Ortiz-Barrientos et al. 2009; Pfennig and Pfennig 2009). Likewise, different patterns of sexual selection can arise between ecomorphs in populations experiencing intraspecific character displacement (Boughman 2002). Such variation among populations in sexual selection can, in turn, potentially cause these populations (or ecomorphs) to diverge from each other even more. Indeed, because of its potential “runaway” nature (Kirkpatrick 1982), sexual selection could continue to promote the elaboration of sexual signals even after there is no longer selection to minimize interactions between species or morphs. Thus, character displacement may initiate divergent trajectories of sexual selection between interacting species and, within species, between allopatric and sympatric populations or between alternative ecomorphs. Sexual selection may then cause the further differentiation of signals and preferences beyond what would have resulted if character displacement were the sole diversifying process (Lande 1982). Thus, diversity in sexual traits is likely maximized when sexual selection and character displacement operate in concert.

Once populations (or ecomorphs) diverge in patterns of sexual selection, the stage is set for speciation. Populations may become so divergent in male signals or female preferences that they fail to recognize each other as acceptable mates and become reproductively isolated (Howard 1993; Hoskin et al. 2005; Pfennig and Ryan 2006; Lemmon 2009; Ortiz-Barrientos et al. 2009; Pfennig and Pfennig 2009). Thus, although character displacement tends to initiate divergence between populations or alternative morphs, sexual selection can further enhance this differentiation, making speciation between them even more likely.

*Phenotypic Plasticity Might Play a Key Role
in Character Displacement*

Finally, Darwin had little to say about the proximate causes of competitively mediated divergence. This is not surprising, given that he knew little about how traits are produced through development and are inherited. However, understanding character displacement’s proximate bases is crucial, because different mechanisms can influence the speed at which new phenotypic variants arise in a population. Because the speed at which new variants arise determines the speed of character displacement (Doebeli 1996), different proximate mechanisms might ultimately influence whether such divergence even occurs in the first place (Pfennig and Pfennig 2009). In particular, any proximate mechanism that facilitates divergence in resource-use or reproductive phenotypes might render character

displacement more likely to transpire, as opposed to competitive or reproductive exclusion. Here, we consider a general and important mechanism for mediating rapid, and potentially adaptive, divergence: phenotypic plasticity.

Phenotypic plasticity—the capacity of a single genome to produce different phenotypes in response to varying environmental conditions (Whitman and Agrawal 2009)—is ubiquitous (reviewed in West-Eberhard 2003; Gilbert and Epel 2009). Darwin clearly recognized that changing environmental conditions could directly induce trait variation among individuals, and he also seems to have grasped the importance of identifying the causes and consequences of phenotypic variation for the evolutionary process. Indeed, in a prefatory notice to August Weismann’s *Studies in the Theory of Descent* (1882; cited in Canfield and Greene 2009), Darwin wrote that “several distinguished naturalists maintain with much confidence that organic beings tend to vary ... independently of the conditions to which they and their progenitors have been exposed; whilst others maintain that all variation is due to such exposure, though the manner in which the environment acts is as yet quite unknown. At the present time there is hardly any question in biology of more importance than this of the nature and cause of variability.”

What Darwin appears to have failed to appreciate, however, is plasticity’s potential role in character displacement. Individual organisms often respond to the presence of other organisms by altering their phenotype adaptively through phenotypic plasticity (Robinson and Wilson 1994; Pfennig and Murphy 2000, 2002; Agrawal 2001; Fordyce 2006). For example, when faced with resource competition or reproductive interactions from a heterospecific, individuals of many species facultatively express traits that lessen competition or reproductive interactions (fig. 2; see also Werner and Hall 1976; Nobel 1997; Losos et al. 2000; Pfennig 2007).

Although such environmentally induced changes in resource-use or reproductive traits were not initially considered to represent character displacement (e.g., see Grant 1972; Arthur 1982; Schluter and McPhail 1992; Schluter 2000), they often satisfy the widely accepted criteria (Schluter and McPhail 1992) for demonstrating character displacement. In particular, experiments have established that these shifts are triggered by the presence of heterospecifics per se (e.g., see fig. 2D) and that they lessen direct competition with heterospecifics for access to resources or mates (e.g., see Pfennig and Murphy 2000; Pfennig 2007). Moreover, these facultative shifts can evolve: experimentally demonstrated shifts in resource-use or reproductive traits often mirror, in magnitude and direction, fixed phenotypic differences observed between naturally occurring populations (e.g., see fig. 2; see also Pfennig 2007) or species (Day et al. 1994; Robinson and Wilson 1994; Losos

et al. 2000; Pfennig and Murphy 2002; Robinson and Parsons 2002; Wund et al. 2008) that have undergone character displacement. Indeed, the magnitude and direction of plastic responses are often genetically variable within natural populations (reviewed in Schlichting and Pigliucci 1998; Windig et al. 2004), suggesting that reaction norms themselves can serve as the targets of selection that diverge between interacting species. In other words, the degree to which individuals facultatively respond to heterospecifics might be the trait that evolves in response to resource or reproductive competition. For example, individuals in sympatry with a heterospecific may evolve different propensities to express traits associated with resource use or reproduction relative to those in allopatry and thereby undergo character displacement (e.g., see Pfennig and Murphy 2000, 2002). Essentially, the ability to respond to heterospecifics in the first place serves as another axis of variation (in addition to more commonly considered morphological, physiological, or behavioral traits) on which selection can act to generate divergence between species. In short, character displacement may often proceed via environmentally induced changes in trait expression.

Phenotypic plasticity might even play a key role in determining the initial rate and direction of character displacement. In particular, character displacement may often unfold as it transitions from an initial phase in which trait divergence is environmentally induced to one in which such divergence is expressed constitutively (see Wilson 1992, p. 174). Although this scenario is not the only way in which character displacement could proceed, it explains why character displacement often appears to unfold rapidly (Fenchel 1975; Diamond et al. 1989; Grant and Grant 2006; Pfennig and Martin 2009). Indeed, when trait divergence is environmentally induced, phenotypic differences between species (and, within species, between populations in sympatry with a heterospecific competitor vs. conspecific populations in allopatry) can arise within a single generation of the focal species; that is, divergence can occur on an ecological timescale (Pfennig and Martin 2009).

The hypothesis that character displacement unfolds as it transitions from an initial phase in which trait divergence is environmentally induced to one in which such divergence is expressed constitutively rests on the long-standing observation that induced phenotypes can lose their environmental sensitivity through the process of genetic assimilation (Waddington 1953). Genetic assimilation occurs when an initially environmentally induced phenotype becomes a constitutively expressed trait (for a recent discussion of evolution by genetic assimilation, see Lande 2009). The loss of plasticity and the subsequent fixation of an induced, divergent phenotype through genetic assimilation can proceed via two routes. First, when main-

tenance or expression of plasticity is costly (Relyea 2002), selection may actively eliminate it (Lahti et al. 2009). Second, plasticity can be lost through mutational degradation or genetic drift (Masel et al. 2007). Essentially, when the members of a population encounter a heterospecific and facultatively express a divergent trait, then the alternative phenotype(s) that more closely resemble(s) the heterospecific's resource-use or reproductive phenotypes would be seldom exposed to selection and might therefore be lost. Experiments have demonstrated the loss of plasticity (Suzuki and Nijhout 2006), and data from natural populations suggest that the resulting differential fixation of alternative phenotypes in different populations can drive character displacement (Pfennig and Murphy 2002).

Phenotypic plasticity might also promote the evolution of genetic differences that fine-tune phenotypic differences between species that arise via character displacement. In particular, once individuals in a population facultatively express a phenotype that lessens costly competitive or reproductive interactions with heterospecifics, selection should favor those alleles or gene combinations that best stabilize, refine, and extend the divergent trait's expression through the process of genetic accommodation (West-Eberhard 2003). Moreover, these environmentally initiated shifts may shield populations from extinction via competitive or reproductive exclusion until more permanent genetic differences between populations and species accumulate.

If the outcome of character displacement depends on initially plastic phenotypes, then phenotypic plasticity in ancestral populations should resemble the constitutively expressed trait differences observed in derived populations that have undergone character displacement. Such a pattern has been found in spadefoot toads (see fig. 2; see also Pfennig and Murphy 2000, 2002; Pfennig and Martin 2010) and sticklebacks (Wund et al. 2008). In both taxa, character displacement appears to have gone through an initial evolutionary phase in which divergence was environmentally induced to a later phase in which divergence has become expressed constitutively. Ancestral plasticity has also been implicated in promoting character displacement in numerous species of freshwater fish (Robinson and Wilson 1994) and *Anolis* lizards (Losos et al. 2000).

The above discussion highlights how plasticity might play a pivotal role in character displacement. Yet the importance of plasticity in character displacement is currently unclear (in part because of historical bias; see above). Relatively few studies have actually explored plasticity's role in mediating trait divergence in response to competition. Now is an ideal time to do so, however, because both character displacement and plasticity are undergoing a resurgence of interest (West-Eberhard 2003; Dayan and Sim-

berloff 2005; Gilbert and Epel 2009; Pfennig and Pfennig 2009; Pfennig et al. 2010).

Conclusions and Future Directions

In developing his principle of divergence of character, Darwin ([1859] 2009) maintained that the origin of species and the evolution of differences between them stem ultimately from divergent selection acting to minimize competitive interactions between initially similar individuals, populations, and species. Although evolutionary biologists have since identified numerous other selective and non-selective processes that can generate diversification and speciation (reviewed in Schluter 2000, 2009; Coyne and Orr 2004; Sobel et al. 2010), character displacement remains an essential part of any general theory for how new species arise and diversify (reviewed in Schluter 2000; Coyne and Orr 2004; Grant and Grant 2008; Pfennig and Pfennig 2009).

Despite character displacement's importance to Darwin's thinking, there are key features that he failed to appreciate. Three in particular stand out. First, Darwin appears to have not understood that selection could also act to lessen reproductive interactions and that such selection could generate divergence rivaling that generated by resource competition. Indeed, reproductive character displacement may be the critical missing link between ecological divergence and the origin of species. Second, he failed to appreciate how divergence is fueled by the intersection of character displacement and sexual selection. Finally, Darwin had little to say about the source(s) of the variation that makes character displacement possible and how the nature of this variation affects the tempo and mode of character displacement. These gaps in Darwin's thinking are the focus of ongoing research. Although more work remains to be done regarding these above issues, two areas in particular are promising.

First, we need to understand more about how character displacement (whether reproductive or ecological) and sexual selection interact. Unfortunately, researchers generally continue to study character displacement and sexual selection separately, as Darwin did. Although these barriers are breaking down, we still lack a fundamental understanding of (1) how interactions between species alter mate choice, male competition, and sexual signaling within species; (2) how such interactions alter the fitness consequences of mate choice and mate attraction; (3) the degree to which sexual selection promotes—or inhibits—divergence in response to competitive interactions between species; and (4) how character displacement and sexual selection interact to promote reproductive isolation between populations within species. By addressing these issues, we will gain greater insight into how and why sexual selection

varies both between and within species (for further discussion, see Ryan 1998; Ptacek 2000; Boughman 2002). We will also better understand sexual selection's role in the origins and maintenance of trait and species diversity.

A second major area requiring attention is the proximate mechanisms that mediate character displacement. Two questions, in particular, stand out. First, what is the source of the phenotypic variation on which selection acts during character displacement? Second, how do different sources of phenotypic variation affect the speed and manner in which character displacement unfolds? Although character displacement is assumed to reflect allelic differences between populations and species, it may alternatively begin with competitively mediated phenotypic plasticity. Indeed, as we explained above, character displacement may often unfold rapidly as it transitions from an initial phase in which species differences arise through phenotypic plasticity to one in which species differences are expressed constitutively.

Additional research into character displacement promises to have far-reaching ramifications. Indeed, because character displacement is central in the origins, abundance, and distribution of biodiversity (reviewed in Schluter 2000; Dayan and Simberloff 2005; Pfennig and Pfennig 2009), understanding character displacement's causes and consequences can shed light onto some of the most fundamental issues in evolutionary biology and ecology, including how new species arise, diversify, and coexist.

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