Sexual Selection and Conflict as Engines of Ecological Diversification

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abstract: Ecological diversification presents an enduring puzzle: how do novel ecological strategies evolve in organisms that are already adapted to their ecological niche? Most attempts to answer this question posit a primary role for genetic drift, which could carry populations through or around fitness "valleys" representing maladaptive intermediate phenotypes between alternative niches. Sexual selection and conflict are thought to play an ancillary role by initiating reproductive isolation and thereby facilitating divergence in ecological traits through genetic drift or local adaptation. Here, I synthesize theory and evidence suggesting that sexual selection and conflict could play a more central role in the evolution and diversification of ecological strategies through the co-optation of sexual traits for viability-related functions. This hypothesis rests on three main premises, all of which are supported by theory and consistent with the available evidence. First, sexual selection and conflict often act at cross-purposes to viability selection, thereby displacing populations from the local viability optimum. Second, sexual traits can serve as preadaptations for novel viability-related functions. Third, ancestrally sex-limited sexual traits can be transferred between sexes. Consequently, by allowing populations to explore a broad phenotypic space around the current viability optimum, sexual selection and conflict could act as powerful drivers of ecological adaptation and diversification.

Keywords: fitness landscape, adaptive landscape, sexual conflict, adaptation, diversification, cross-sexual transfer, sexual dimorphism.

Introduction

Organisms occupy a spectacular diversity of ecological niches, but the causes of ecological diversification present a puzzle (Coyne et al. 1997; Coyne and Orr 2004; Lynch 2010). Natural selection is "shortsighted," favoring the best of the currently available alternatives (Darwin 1859; Fisher 1930), and should therefore oppose divergence from established niche-exploitation strategies because intermediate phenotypes between alternative niches are typically maladaptive. This problem is conventionally represented

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as the paradox of peak shift on a "fitness landscape" (Coyne and Orr 2004; Gavrilets 2004; Pigliucci and Kaplan 2006). If the environment and the associated selection pressures remain constant, then in order to diversify from one peak (i.e., local optimum) to another, the population must first traverse a fitness valley—a range of maladapted intermediate phenotypes—to reach the unstable saddle point between adjacent peaks. Wright (1932), who first formalized this problem, famously noted that "there must be some trial and error mechanism on a grand scale by which the species may explore the region surrounding the small portion of the field which it occupies" (p. 359). Wright (1931, 1932) and many subsequent thinkers (see Coyne and Orr 2004) invoked genetic drift as that trial-and-error mechanism. However, empirical studies have yielded little evidence that genetic drift plays an important role in morphological evolution (Coyne et al. 1997; Coyne and Orr 2004). The mechanisms that could drive ecological diversification thus remain poorly understood.

Sex-specific selection represents an alternative to genetic drift as a mechanism of ecological diversification, but this possibility remains largely unexplored. Evolution is often modeled as the movement of a population across a fitness landscape that represents the relationship between the population-mean phenotype and the population-mean fitness and whose topography diverges increasingly from that of the individual fitness function as phenotypic variance increases (Whitlock 1995; Borenstein et al. 2006). Selection pushes the population-mean phenotype toward the local peak on this landscape (Pigliucci and Kaplan 2006). Sex complicates this model because sexual populations consist of two genetically and ecologically interconnected subpopulations (i.e., the two sexes) that experience a combination of common and divergent selection vectors.

The study of niche shifts is concerned with changes in the strategy for survival and resource exploitation within the environment (Pianka 2000)—novel types of feeding apparatus, locomotory adaptations, ways of evading predators, and so forth. Most aspects of this ecological strategy are typically common to both sexes, and this is reflected

in a common phenotypic optimum for survival and resource exploitation within the niche (but see Shine 1989; Bolnick and Doebeli 2003; Butler et al. 2007). These requirements can be referred to collectively as "viability" (see Lande and Kirkpatrick 1988). But, as Darwin (1859, 1871) pointed out, male sexual competition generates sexual selection that tends to displace males from the optimum phenotype for viability. Sexual selection on males can also result in sexual conflict, reflected in sexually antagonistic selection on many traits in the sexes (Parker 1979; Lande 1980, 1987). While sex-specific selection can also reflect female-limited functions associated with offspring production (Rice and Chippindale 2001) or resource partitioning among sexes (Butler et al. 2000, 2007), sexual and sexually antagonistic selection are particularly interesting because they can be very powerful, often strongly oppose viability selection, vary both within and among species, and generate complex dynamics of sexual coevolution (Andersson 1994; Iwasa and Pomiankowski 1995; Arnqvist and Rowe 2005; Gavrilets and Hayashi 2006; Svensson et al. 2006).

Thus, excepting more complex cases where the sexes occupy distinct ecological niches (Shine 1989; Bolnick and Doebeli 2003; Butler et al. 2007), sexual populations can be regarded as evolving on a fitness landscape whose topography reflects the combination of a "viability landscape" that is largely common to the sexes and sex-specific selection vectors reflecting sex differences in reproductive strategy, of which sexual and sexually antagonistic selection may typically diverge most strongly from the viability optimum (fig. 1). To account for ecological diversification, it is necessary to explain why populations undergo shifts on the viability landscape from a local viability peak (current niche) to a new viability peak (new niche). Could sexual and sexually antagonistic selection facilitate such population shifts across viability valleys to alternative viability peaks (see Lande and Kirkpatrick 1988; Miller 1994; Miller and Todd 1995)?

Sexual selection and conflict are seen as important diversifying processes (Gavrilets 2000; Panhuis et al. 2001; Coyne and Orr 2004; Dieckmann and Doebeli 2004; Svensson et al. 2006) but are generally assumed to play a direct role only in the diversification of traits involved in sexual competition and mating ("sexual traits"), such as sexual signals and weapons (Andersson 1994), genitalia (Eberhard 2010), accessory-gland products (Wolfner 1997), and sperm (Kleven et al. 2008). In the evolution and diversification of traits that function to enhance survival or resource acquisition ("viability traits"), sexual selection and conflict are assumed to play an indirect and ancillary role (but see Lande and Kirkpatrick 1988; Miller 1994; Miller and Todd 1995). In this role, sexual selection and conflict are seen as potentially facilitating or impeding adaptive
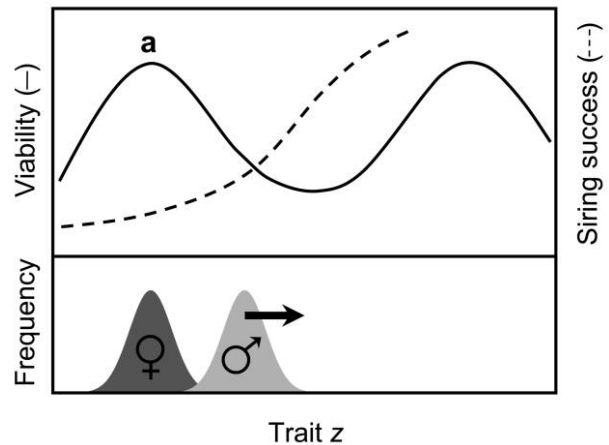

Figure 1: Sexual selection and the ecological niche. A hypothetical "viability landscape" (solid curve), reflecting the relation between a population's mean phenotype and mean fitness, is represented as having two peaks denoting alternative viability optima for a trait z. A population occupies viability peak a, but sexual selection on males (dashed curve) favors an increase in the mean size of trait z, causing males (light gray phenotypic distribution) to evolve away from peak a (solid arrow). Sexual selection on males can also generate sexual conflict, thereby displacing the mean phenotype of females (dark gray phenotypic distribution) from peak a as well (see text). Sexual selection can thereby cause the population-mean phenotype to evolve away from the local viability peak.

evolution, whose course is determined by viability selection within the ecological niche (see Candolin and Heuschele 2008; Maklakov et al. 2009, 2010; Labonne and Hendry 2010; fig. 2). As Darwin (1859, 1871) pointed out, sexual selection often appears to act at cross-purposes to viability selection (although cases where sexual and viability selection are concordant may be easy to overlook), and sexual traits typically impose viability costs on their bearers (Kotiaho 2001). But sexual selection could also promote "good genes" for viability (Zahavi 1975; Nur and Hasson 1984; Proulx 2002; Lorch et al. 2003) or, conversely, contribute to the purging of deleterious mutations (Agrawal 2001). Sexual conflict is assumed to impede ecological adaptation by displacing one or both sexes from their phenotypic optima (Parker 1979; Lande 1980; Chippindale et al. 2001; Arnqvist and Rowe 2005; Kwan et al. 2008; Bonduriansky and Chenoweth 2009). Sexual selection and conflict are also considered to promote reproductive isolation between populations, thereby facilitating divergence through genetic drift and/or local adaptation (Gavrilets 2000; Panhuis et al. 2001).

The ancillary role ascribed to sexual selection and conflict in ecological adaptation and diversification reflects the prevailing view of sexual traits as distinct entities whose functions are limited to a sexual context (e.g., see Civetta
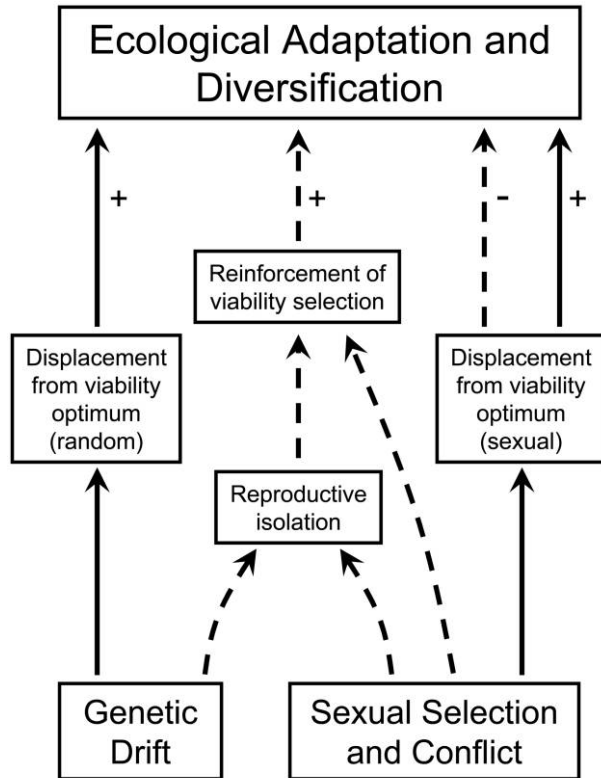
Figure 2: Potential effects of genetic drift and sexual selection/conflict on ecological adaptation and diversification. Solid arrows represent effects on both the rate and the direction of ecological change, whereas dashed arrows represent effects on its rate only. Plus signs denote effects that can promote ecological adaptation and diversification, whereas minus signs denote effects that can interfere with this process. Ecological co-optation is represented by the solid arrow with plus sign on the left side of the diagram (see text for further explanation).

and Singh 1998; Green 2000; Salzburger 2009; Tobias and Seddon 2009)—a dichotomy that originated with Darwin (1859, 1871). However, many features of the phenotype serve a combination of sexual and viability functions. Moreover, although some traits may be appropriately categorized as having "sexual" or "viability" functions at a given point in evolutionary time (e.g., see Gibbs 1998; Salzburger 2009; Abbott et al. 2010; Arnegard et al. 2010), separating the roles of sexual and viability functions in a trait's evolutionary history can be extremely difficult (see Murphy 1998; Estrada and Jiggins 2008; Maan and Cummings 2009). Rather, in the context of long-term evolution, the entire phenotype (and the developmental-genetic systems that shape it) is more appropriately viewed as a multipurpose tool kit in which the functions of various components can change over time (True and Carroll 2002).

It has long been recognized that viability traits can be co-opted for sexual functions ("sexual co-optation")—for example, appendages such as legs or antennae can be modified for combat, courtship, or sexual grasping functions (Kawano 1997; Sivinski 1997; Emlen and Nijhout 2000; Westlake et al. 2000). Oddly, the converse process—the co-optation of sexual traits for novel viability functions ("ecological co-optation")—has rarely been considered. It has been suggested that female mate preferences can select in arbitrary directions on male signals and thereby cause populations to evolve away from the local viability peak and, in some cases, to diversify to a new peak representing a novel ecological strategy (Lande and Kirkpatrick 1988; Miller 1994; Miller and Todd 1995). However, this idea has received very little attention and has not been reexamined in light of recent advances in understanding of sexual selection and conflict or of the developmental-genetic basis of sexually dimorphic traits.

Below, I synthesize existing theory and evidence to make the case that ecological co-optation offers a plausible hypothesis for the adaptive evolution of a diverse range of ecological niche-exploitation strategies in sexually reproducing species. Through this process, sexual selection and conflict could play a direct role in ecological adaptation and niche shift (fig. 2). Below, I outline the three major premises on which the ecological-co-optation hypothesis is based: the tendency for sexual coevolution to displace populations from their local viability optimum, the potential for sexual traits to serve as preadaptations for novel viability-related functions, and the possibility of cross-sexual transfer of ancestrally sex-limited traits. I then consider the predictions of the ecological-co-optation hypothesis, and discuss some potential examples.

Ecological Co-optation of Sexual Traits

The possibility of ecological co-optation rests on three main premises (summarized in table 1). Below, I outline these premises and the evidence and ideas on which they rest.

Sexual Selection and Conflict Can Displace Populations from Their Local Viability Optimum

For ecological diversification to take place, a population must be displaced from its local viability peak (Wright 1932; Coyne and Orr 2004; Gavrilets 2004). Theory and evidence show that sexual selection and conflict can cause such displacement. Sexual selection can promote the evolution of sexual traits that reduce the viability of individuals expressing those traits (Darwin 1859, 1871; Andersson 1994). For example, the evolution of male-limited sexual weapons or displays can displace males from their viabil-

Table 1: Premises of the ecological-co-optation hypothesis and the type of analysis required to test them

	Premise	Analysis
1.	Sexual selection and conflict can displace populations from their viability optimum. Moreover, these processes typically favor distinct phenotypes in the sexes (sexual dimorphism). Sexual selection and conflict thereby enable populations to explore a wide phenotypic space around the local viability peak.	Ecological, experimental
2.	Sexual traits can serve as preadaptations for novel viability-related functions in a changing environment or a new niche. Such traits can then evolve into mixed-function traits or lose their ancestral sexual function and become dedicated viability-enhancing traits.	
3.	An ancestrally sex-limited trait can evolve to be expressed in the other sex through the cross-sexual transfer of a developmental-genetic pathway. Sex-limited sexual traits that provide preadaptations for novel viability-related functions can thereby evolve to be expressed in the other sex.	Developmental-genetic, experimental

ity-selected phenotypic optima for a variety of morphological, life-history, behavioral, and physiological traits. This can occur because males expressing the sexual trait will reap sexual benefits (i.e., increased siring success) that compensate for the viability costs. Moreover, sexual conflict can promote the evolution of traits that also reduce viability of individuals of the opposite sex (but without compensating sexual benefits) and thereby, in principle, drag entire populations into viability valleys characterized by reduced mean recruitment and elevated probability of extinction (Parker 1979; Kokko and Brooks 2003; Arnqvist and Rowe 2005; Rowe and Day 2006). Under intralocus sexual conflict, sex-specific selection (e.g., sexual selection on males) displaces homologous traits in the other sex from their viability optima as a result of intersexual genetic correlation for these traits (Lande 1980; Chippindale et al. 2001; Kwan et al. 2008; Bonduriansky and Chenoweth 2009). Intralocus sexual conflict can affect the evolution of a diverse range of traits, including body size and shape (Rice and Chippindale 2001; Prasad et al. 2007; Abbott et al. 2010), brain structure (Jacobs 1996), behavior (Bedhomme et al. 2008; Maklakov et al. 2008), activity level (Long and Rice 2007), immunity (Rolff 2002; Svensson et al. 2009), and life history (Promislow 2003; Bonduriansky et al. 2008). Under interlocus sexual conflict, male-male competition interferes directly with the female reproductive strategy by inflicting injury or preventing optimal acquisition or allocation of reproductive resources. Interlocus sexual conflict can generate a "sexual arms race" involving the evolution of distinct sexually antagonistic traits in each sex (Parker 1979; Arnqvist and Rowe 2005). Sexual selection and conflict can also engender Red Queen dynamics that drive trait evolution in arbitrary and continually changing directions (Iwasa and Pomiankowski 1994, 1995; Gavrilets et al. 2001; Gavrilets and Hayashi 2006).

Sexual selection and sexual conflict thus give rise to an enormous diversity of morphological, behavioral, physi-

ological, and life-history traits that function at cross-purposes to current viability needs (Darwin 1871; Andersson 1994; Miller 1994; Miller and Todd 1995; Arnqvist 1998; Gavrilets 2000; Arnqvist and Rowe 2005; Gavrilets and Hayashi 2006). Yet by allowing evolution to deviate in arbitrary directions from the local viability optimum, sexual selection and conflict may actually free populations from an important evolutionary constraint, permitting the evolutionary "exploration" of a phenotypic space broader than viability selection alone would allow (Lande and Kirkpatrick 1988; Miller 1994; Miller and Todd 1995).

Sexual Traits Can Serve as Preadaptations for Viability-Related Functions

Theory also suggests that traits that evolve to serve sexual functions can sometimes furnish preadaptations for novel viability-related functions (see Lande and Kirkpatrick 1988; Miller 1994; Miller and Todd 1995). Empirical evidence supports the possibility of such shifts in function because many phenotypic features play a combination of sexual and viability-related roles, as shown by numerous studies of behavior (Snook et al. 2005), sensory systems (Norry et al. 1999), immunity (Restif and Amos 2010), life history (Clinton and Le Boeuf 1993), and body size and shape (Abbott et al. 2010). For such features, evolution in a sexual context can readily influence function in a viability-related context. Moreover, as shown by the examples outlined in a later section, any type of trait (including traits typically associated with sexual selection, such as bright colors and weapons) has the potential to function in a viability-related role. Traits that evolve in the context of sexual selection and conflict can therefore be seen as part of a population's general evolutionary "tool kit" that can be put to use in a viability-related role in a suitable environment. Preadaptation could occur in two ways.

First, a change in ambient conditions could lead to cir-

cumstances where an existing sexual trait begins to enhance viability (e.g., survival or access to resources). For example, a change in species-community composition could lead to a sexual display of bright colors becoming advantageous as an incipient aposematic signal (see Maan and Cummings 2009) or signal mimic (see Jiggins et al. 2001, 2004). A sexual weapon could become advantageous in competition for food resources or defense against predators (see Espmark 1964; Otronen 1988; Watson and Simmons 2010*c*). A sexually selected cuticular hydrocarbon (CHC) phenotype could confer enhanced resistance to desiccation in a drying environment (see Kwan et al. 2008; Kwan and Rundle 2010).

Second, evolution of a sexual trait could eventually (once a certain phenotypic threshold is passed) produce a phenotype that allows individuals to exploit a new niche. This possibility is supported by existing theory based on the coevolution of female preferences and male displays. Miller and Todd (1993) used simulations to show that the coevolution of preference and display could "cause populations to wander capriciously through phenotype space" (p. 21) and drive the population-mean phenotype away from the local viability optimum. They argued that such coevolutionary dynamics could allow populations to "search" phenotypic space around the local viability optimum and occasionally stumble onto new ecological innovations, leading to ecological diversification (Miller 1994; Miller and Todd 1995).

Earlier, Lande and Kirkpatrick (1988) had modeled a similar process of preference-display coevolution, but with the additional assumption of an intersexual genetic correlation between the male display trait and its female homologue. They found that female preference on the male trait can drag the mean phenotypes of both males and females off the viability peak (peak a in fig. 3)—that is, generate intralocus sexual conflict. Moreover, sexual selection can result in a broad zone of instability between viability peaks, and if the trait mean for males (or both sexes) moves into this unstable region, then the population can evolve rapidly across the viability valley (under a combination of sexual and viability selection) to a new peak (peak b in fig. 3). In essence, by creating a line of equilibria where sexual and viability selection balance, sexual selection can flatten a region of the (net) fitness landscape between viability peaks. Lande and Kirkpatrick's (1988) model is a special case of the general mechanism of peak shift via correlated response to selection, whereby an ecologically important trait is dragged across a fitness valley by selection acting on another trait with which it is genetically correlated (Price et al. 1993). Whereas Price et al. (1993) considered correlated evolution of traits within the same sex, Lande and Kirkpatrick (1988) envisioned
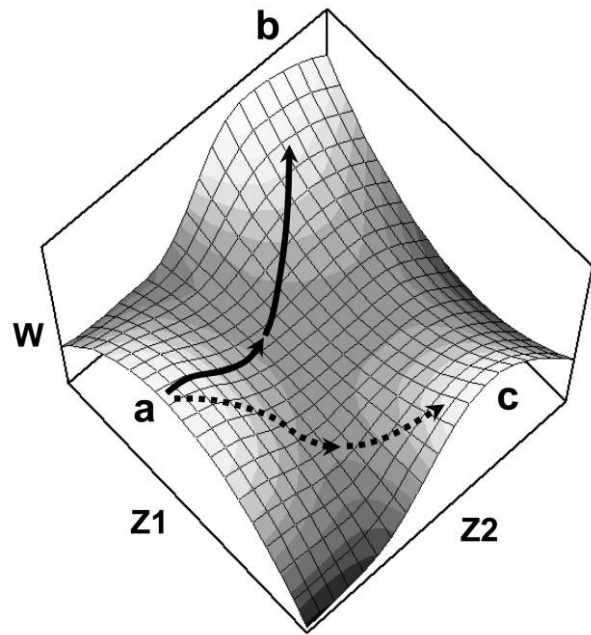

Figure 3: Hypothetical role of sexual selection and conflict in driving ecological adaptation and diversification. A "viability landscape" is represented in two phenotypic dimensions (Z1 and Z2) and fitness (W) and has three peaks, representing alternative viability optima that correspond to distinct ecological niches. A population located on peak a experiences a new mode of male-male sexual competition that generates intralocus sexual conflict, causing both males and females to evolve away from the viability peak. Having reached the unstable saddle point between peaks a and b, the population (or a new host race) then ascends to peak b (solid arrows). If male-male sexual competition imposes direct costs on females (interlocus sexual conflict), then selection could also drive the evolution of defensive traits in females, thereby displacing females from peak a toward peak c (dashed arrows).

correlated evolution of a female trait in response to sexual selection on the trait's homologue in males.

Intuitively, consider an insect population where sexual selection on males favors elongated legs for grasping females. Under sexual selection, the mean leg length of males could increase until it becomes sufficient to permit the exploitation of a new ecological niche, such as foraging on rough-textured or wet surfaces. Although, in order for this to occur, the mean male phenotype has to pass through an intermediate region between alternative niches, the decline in viability will be compensated for by enhanced mating success. If the intersexual genetic correlation for leg length is high and sexual selection on males is sufficiently strong to compensate for viability costs to females, then sexual selection on males can also drag females across the region of low-viability intermediate phenotypes, allowing them to shift to the new niche.

These insights can be generalized to encompass inter-locus sexual conflict as well as intralocus sexual conflict. Under interlocus sexual conflict, each sex employs a different set of sexually antagonistic traits (affected by different genetic loci) to pursue its reproductive strategy. Thus, starting with a sexually monomorphic population occupying a viability peak (peak a in fig. 3), sexual selection can drive evolution of a male sexual trait that displaces males into the viability valley between peaks a and b (fig. 3). As in the above example, sexual selection may favor elongated legs in males for grasping females. However, if this male trait causes collateral harm to females (e.g., by elevating female mating rate above the optimum), then females may evolve a defensive trait (such as elongated wings to facilitate escape from males), and this could result in the displacement of the mean female phenotype into the viability valley between peaks a and c (fig. 3). Moreover, because sexually antagonistic traits may be subject to intersexual genetic correlation, interlocus sexual conflict may generate novel intralocus sexual conflicts (Bonduriansky and Chenoweth 2009). In the current example, this could result in the evolution of elongated legs and wings in both sexes, and both traits could provide potential preadaptations for novel viability-related functions.

If a sexual trait comes to serve as a preadaptation for a novel viability-related function, it may subsequently evolve, under viability selection, to function in a viability-related role. The trait may then continue to function in its ancestral role and become a multifunction trait. For example, if a male sexual weapon acquires a secondary function in antipredator defense in one or both sexes, it may continue to function in sexual competition as well (see Espmark 1964; Otronen 1988; Watson and Simmons 2010c). Such traits may, however, evolve toward a phenotype that reflects a compromise between the trait's sexual and viability functions, which are likely to select somewhat differently on the trait. Alternatively, the new viability-related role may be incompatible with the original sexual role, and if viability selection is sufficiently strong, the trait may lose its original sexual function and become a dedicated viability-enhancing trait. Such a fate may be likely for sexual displays. For inter- or intrasexual displays to convey honest signals of mate quality or resource-holding capacity, they must be sufficiently variable to allow for accurate assessment by potential mates or rivals. If a sexual signal acquires a viability-related function (e.g., as an aposematic signal), this may generate strong stabilizing selection on the signal (Debat and David 2001; Siegal and Bergman 2002), and at the same time the signal may become less costly to express because it enhances rather than reduces viability. Consequently, the signal's condition-dependent phenotypic variability may eventually be reduced to the point where its utility in sexual signaling (i.e.,

honesty) is lost. The signal may then become dedicated for its viability-related function, and a new sexual signal may evolve in its place—a process superficially resembling "chase-away" sexual coevolution (Holland and Rice 1998).

Traits Can Be Transferred between Sexes

An ancestrally sex-limited trait may evolve to be expressed in the other sex as well—a process called cross-sexual "transfer" (Darwin 1871; West-Eberhard 2003) or "transvestism" (Clarke et al. 1985). Darwin (1871) regarded cross-sexual transfer as a nonadaptive by-product of what is now called intersexual genetic correlation, but it is clear that selection could favor cross-sexual transfer of traits that furnish preadaptations for novel viability-related roles. Defined more precisely, cross-sexual transfer is an evolutionary process whereby an ancestrally sex-linked developmental pathway (i.e., a pattern of transcription and regulation activated in one sex as part of the sex-determining developmental cascade initiated by the sex chromosomes or sex-determining factors) comes to be incorporated in the developmental program of the other sex. After transfer, the ancestrally sex-linked developmental pathway is initiated in a way that is no longer sex dependent, allowing the trait to be expressed in both sexes (although sex-specific modifiers may evolve to optimize the trait's expression within each sex). For example, an ancestrally male-limited sexual trait may be transferred to females, resulting in a female homologue regulated by a developmental-genetic architecture of common origin with the male trait. In this way, an ancestral state of sexual dimorphism may evolve toward a monomorphic state of "mutual ornamentation" (see Miller and Todd 1995; Oliver and Monteiro 2011). Many examples of apparent cross-sexual transfer are available, involving a diverse array of traits and taxa (Darwin 1871; Clarke et al. 1985; Wcislo 1999; West-Eberhard 2003; Reinhardt et al. 2007; Aguiar Colonello-Frattini et al. 2010).

Cross-sexual transfer may allow the expression of a newly evolved trait to be canalized through selection on one sex before transfer to the other sex. For example, the development of an ancestrally male-limited sexual trait would be fine-tuned (e.g., optimized in relation to body size) and buffered against genetic and environmental perturbations over many generations of expression and selection in males. Because of its evolutionary history in males, such a trait would perhaps be more likely to enhance fitness when newly expressed by a female.

Importantly, both theory (Rhen 2000, 2007; Day and Bonduriansky 2004; Coyne et al. 2008; Bonduriansky and Chenoweth 2009) and empirical evidence (Kopp et al. 2000; Williams et al. 2008) suggest that sex-specific development can be regulated by relatively simple genetic

"switch" mechanisms that could be deactivated via a small number of genetic changes. A particularly well-studied example is the developmental-genetic regulation of sexual dimorphism in abdominal pigmentation of *Drosophila*. In *Drosophila melanogaster* males, pigment is expressed on the posterior abdomen, but pigment expression is suppressed in females by a regulatory gene (*bric-a-brac*) whose transcription is upregulated by the female-specific isoform of *doublesex*, which regulates sex-specific somatic development (Kopp et al. 2000). The evolution of male-limited pigmentation in *D. melanogaster* involved changes in the domain of expression of two *cis*-regulatory elements, both of which were already involved in the control of other sexually dimorphic traits (Williams et al. 2008). Moreover, abdominal pigmentation varies in sex-specificity of expression among closely related drosophilid species, and it appears that the evolutionary transition between monomorphic and dimorphic expression could occur through selection on standing genetic variation (Kopp et al. 2000; Williams et al. 2008). The sex-specificity of trait expression appears to be equally evolutionary labile in many other taxa (e.g., Burns 1998; Badyaev and Hill 2003; Emlen et al. 2005; Ord and Stuart-Fox 2006; Oliver and Monteiro 2011). Indeed, the relative simplicity and lability of the mechanisms that control sex-specific development is attested to by the capacity of many parasites to induce partial or complete sex change in the host (Salt 1927; Wulker 1964; Werren 1997; Wcislo 1999). It is thus plausible to conjecture that sexually monomorphic expression could evolve (perhaps quite rapidly) from an ancestrally dimorphic state via a process of cross-sexual transfer.

The dynamics of sex-specific trait evolution and cross-sexual transfer may be complex. Sexually homologous traits often exhibit high intersexual genetic correlations, but divergent selection on homologous traits in the sexes favors modifications to the genetic architecture that reduce the intersexual genetic correlation, allowing sexual dimorphism to evolve (Lande 1980, 1987; Rhen 2000, 2007; Day and Bonduriansky 2004; Bonduriansky and Chenoweth 2009). Thus, when a trait evolves through sexual selection on males, the saddle point between alternative ecological niches may be reached initially by males or by both sexes almost simultaneously, depending on the initial strength of the intersexual genetic correlation and its rate of decay under divergent selection (Lande and Kirkpatrick 1988). If a trait favored by sexual selection in males rapidly evolves male-limited expression but subsequently begins to confer viability benefits for males, then selection may favor its expression in females as well. Under interlocus sexual conflict, where each sex evolves distinct sexually antagonistic traits, cross-sexual transfers could, in principle, occur in both directions.

Each of the three premises outlined above is therefore supported by theory and empirical evidence. Ecological co-optation is a corollary of the combination of these premises: sexual selection and conflict often act at cross-purposes to viability selection, thereby displacing populations from the local viability optimum. Moreover, such displacement occurs along multiple, sex-specific dimensions, reflecting the evolution of distinct sexual traits in each sex. Because many aspects of the phenotype serve a combination of sexual and viability-related functions and virtually every trait has the potential to do so, sexual traits can furnish preadaptations for novel viability-enhancing roles. Finally, ancestrally sex-limited traits can be transferred to the other sex. Sexual traits can thereby be co-opted for novel viability-related functions. Below, I consider what evolutionary signatures the ecological-co-optation process might produce if it occurs. These predictions can be used to test the hypothesis and gauge its importance as a mechanism of ecological diversification.

Predictions of the Ecological-Co-optation Hypothesis

Ecological co-optation will give rise to characteristic macroevolutionary patterns that could be detected through comparative phylogenetic analysis. An evolutionary signature of this process within a clade is the occurrence in both sexes of some species of an ancestrally sex-limited sexual phenotype. Where detailed information on trait function is available, evolutionary shifts in trait function from sexual in ancestors to viability related in descendants will be detected (box 1; fig. 4). Some evidence of such patterns is discussed in the next section.

Tests of these predictions face at least two challenges. First, it is necessary to find an appropriate evolutionary timescale for analysis. Depending on the taxonomic group, shifts from sexual to viability-related trait function and from dimorphic to (more) monomorphic expression could be detectable via comparison of multiple populations of a single species, multiple species within a genus, or related species groups. In some taxa, such changes may occur rapidly enough to be observable within the span of artificial-evolution experiments. Second, where females express a trait that resembles an ancestrally male-limited sexual trait, it is necessary to eliminate the possibility of independent, convergent evolution of the trait in the sexes (West-Eberhard 2003). This requires a detailed knowledge of the developmental genetics of the trait in both sexes.

The ecological-co-optation hypothesis also yields the general prediction that the rate or extent of ecological diversification within a clade will reflect the intensity of sexual selection and conflict (see Miller and Todd 1995). No studies (to my knowledge) have addressed this question directly, but some studies have asked related questions. Several studies have shown that taxa exhibiting

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Box 1: Predictions of the ecological-co-optation hypothesis

1. Within groups of related species, some phenotypes occur as sex-limited sexual traits in some species but as sexually monomorphic traits in other species.
2. Evolutionary transitions occur from dimorphic to monomorphic trait expression, whereby an ancestrally sex-limited sexual trait is transferred to the other sex as a viability-enhancing trait.
3. Lineages characterized by more intense sexual selection and conflict exhibit greater ecological diversity, "ecological plasticity," and, perhaps, species richness than lineages characterized by weaker sexual selection and conflict. This may result in a positive association among lineages between the propensity to evolve sexual dimorphism and the rate of population splitting and speciation.
4. The initial stages of ecological diversification through the co-optation of sexual traits can occur in large populations, which can give rise to ecologically distinct daughter populations.

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stronger sexual selection (reflected in greater sexual dimorphism) have elevated probabilities of extinction or reduced probabilities of successful invasion (McLain et al. 1995; Sorci et al. 1998; Doherty et al. 2003; Morrow and Pitcher 2003), although this is not a universal pattern (Morrow and Fricke 2004). These studies generally support the individual- and population-level costs of sexual selection and conflict but do not assess effects on the long-term evolutionary potential for ecological diversification. In an evolutionary context, theory suggests that sexual selection and conflict could either increase or reduce the rate of ecological adaptation (see fig. 2 and "Introduction"), with the net effect perhaps dependent on details of the ecology and mating system. A recent review of the empirical evidence found no clear overall pattern (Candolin and Heuschele 2008). However, research on this question has typically considered sexual selection's effects on rates of adaptation occurring in response to ecological factors rather than sexual selection's potential to create novel ecological opportunities through preadaptation. Interestingly, in some birds, sexual selection and conflict intensity appear to covary positively with "ecological plasticity"—the range of environments that a population can occupy (Badyaev and Ghalambor 1998; Tobias and Seddon 2009)—a pattern consistent with ecological co-optation. Further studies are needed to test for an association between sexual selection intensity and ecological diversification on a long-term, evolutionary timescale.

Notably, the ecological-co-optation hypothesis yields several predictions that contrast with predictions based on genetic drift. First, whereas evolution by genetic drift is expected to occur only in small populations (Coyne and Orr 2004), ecological co-optation can be initiated in large populations as well (Lande and Kirkpatrick 1988). Second, compared with drift, ecological co-optation may result in a greater degree of ecological differentiation between sister taxa, because sexual selection and conflict often favor divergence in reproductive characters (Iwasa and Pomiankowski 1995; Arnqvist 1998; Holland and Rice 1998; Gavrilets 2000; Gavrilets and Hayashi 2006) and because such characters can furnish ecological preadaptations (Miller

and Todd 1995). Third, in contrast with drift, ecological co-optation will produce derived ecological strategies that resemble the secondary sexual traits of ancestors. Fourth, unlike genetic drift, sexual selection and conflict could produce long-term evolutionary trends, with potentially important consequences for ecological strategy (Miller and Todd 1995; West-Eberhard 2003).

The ecological-co-optation hypothesis also contrasts in a key prediction with the "ecological sexual dimorphism" model, whereby dimorphism evolves as a form of "competitive displacement" that reduces competition between sexes over food or other ecological resources (Slatkin 1984; Shine 1989; Bolnick and Doebeli 2003). Theory shows that the evolution of dimorphism via competitive displacement represents an alternative to population splitting or speciation as a "solution" to the ecological "problem" posed by intraspecific resource competition, such that "sexual dimorphism and speciation are mutually antagonistic out-
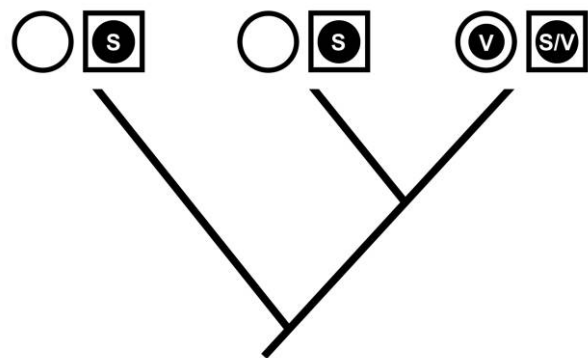

Figure 4: A predicted evolutionary signature of ecological co-optation. Open circles represent females, open squares represent males, and branch tips represent populations or species. The filled circles represent an ancestrally male-limited trait with sexual function (S) that is subsequently co-opted for viability-related function (V) and transferred to females. After ecological co-optation, the trait serves a purely viability-related function in females but a combination of sexual and viability-related functions in males.

comes of frequency-dependent disruptive selection" (Bolnick and Doebeli 2003, p. 2443). This model therefore predicts a negative association among lineages between the propensity to evolve sexual dimorphism and the rate of population splitting or speciation (Bolnick and Doebeli 2003). In contrast, ecological co-optation would tend to produce the opposite pattern, in that those lineages that are most prone to sexual selection and conflict would tend to evolve sexual dimorphisms (at least transiently) as well as undergo ecological diversification and niche shift. Because the evolution of a "niche polymorphism" is a precondition for population splitting and speciation under sympatry (Coyne and Orr 2004), ecological co-optation may be expected to result in a positive association among lineages between sexual dimorphism and speciation (see below for further discussion of this issue). It is, of course, possible that ecological co-optation, competitive displacement, and drift are acting simultaneously, so that observed patterns will reflect their relative importance in the evolution of a given lineage.

Examples of Traits That May Evolve via Ecological Co-optation

Below, I outline some examples of traits for which ecological co-optation provides a plausible evolutionary hypothesis. Further work is required in each case to test this hypothesis definitively.

Weapons

In several groups, females possess weapons that function in intraspecific resource competition and resemble ancestrally male-limited sexual traits. Although the evolution of female weapons does not necessarily entail a niche shift, it does represent an altered foraging strategy, involving intensified female-female competition over food patches. The potential for some females to monopolize food resources could be associated with an altered distribution of individuals in the environment and could select for alternative foraging strategies or diet preferences in poor-condition females that are excluded from their ancestral resources.

In many species of beetles, males express horns on the head and/or pronotum and use these structures as weapons in competition for mates (Emlen et al. 2005). However, in a number of species, horns occur in females. Emlen et al. (2005) identified 13 independent instances of females gaining horns within the dung beetle genus *Onthophagus*. Of these, female horns appeared in the phylogeny simultaneously with male horns in 10 cases. In three other cases, females gained horns independently of males, but such gains invariably occurred in lineages where similar horns

occurred ancestrally in males. Moreover, seven of the instances where females gained horns were associated with high population densities, perhaps reflecting high levels of female-female aggression. Subsequent investigations on one such species, *Onthophagus sagittarius*, failed to find any evidence that female horns function as a female sexual display used in male mate choice (Watson and Simmons 2010*b*) but instead showed that females use their horns in competition for oviposition resources (Watson and Simmons 2010*c*). A resource-competition function for female horns has also been reported in the carrion beetle *Coprophanaeus ensifer* (Otronen 1988).

In cervids, antlers are typically expressed in adult males and used as weapons and signals in competition for mates. However, in the caribou (*Rangifer tarandus*), antlers are also expressed in females, which retain their antlers later into the season than do adult males and are thereby able to achieve high social status during winter, when food is most scarce (Espmark 1964). Pregnant females, in particular, retain their antlers until after calving and use them to defend food resources for themselves and their newborn calves (Espmark 1964).

Evolution of female weapons in these lineages therefore furnishes plausible, independent examples of ecological co-optation. Further work is needed to establish whether weapon expression has a common genetic and developmental basis in the sexes. In *O. sagittarius*, horn development is more strongly condition dependent in males than in females, and there is no evidence of intersexual genetic correlation for horn length (Watson and Simmons 2010*a*). However, sex differences in condition dependence could reflect effects of sex-specific modifiers of horn expression, while intersexual genetic correlation may be obscured by strong environmental effects on male horn length. It is unclear whether the initial stages of female weapon evolution in these species were associated with sexual conflict, although the costs of horn expression appear to be low for *O. sagittarius* females (Simmons and Emlen 2008), suggesting that intralocus sexual conflict over horn expression may have been weak in this lineage.

Coloration

In diverse taxa, color patterns that currently serve viability-related functions such as aposematic signaling, mimicry, or camouflage may have evolved via ecological co-optation of sexual signals. There is a need for further work on the evolutionary history and developmental-genetic basis of these traits.

In birds, sexually monomorphic coloration often reflects bright coloration in females as well as males, and phylogenetic analyses suggest that most transitions from sexually dimorphic to monomorphic coloration appear to involve

females acquiring malelike color patterns (Irwin 1994; Burns 1998; Badyaev and Hill 2003)—a pattern that conflicts with the assumption that male sexual displays are costly and opposed by viability selection in females (Badyaev and Hill 2003). Malelike plumage can evolve in females via mutual mate choice (Kokko and Johnstone 2002), but this explanation conflicts with evidence that losses/gains of bright colors often occur before losses/gains of sexual preference (Wiens 2001). These paradoxical patterns led Badyaev and Hill (2003) to invoke genetic drift as an explanation for such transitions. But an alternative explanation is that malelike plumage is acquired by females for a viability-related function. Although bright plumage is generally considered to enhance male mating success at the cost of reduced viability (e.g., through increased visibility to predators or costly investment in pigments), bright colors can, in some cases, serve to startle or warn predators (Protas and Patel 2008; Stevens et al. 2008), provide camouflage (Marshall 2000), or function in female-female competition for resources (Irwin 1994; Heinsohn et al. 2005).

Poison frogs typically exhibit bright colors as aposematic warning signals. In *Oophaga pumilio*, considerable variation in brightness and hue occurs both within and among populations, and experiments have shown that the same bright colors serve as both aposematic signals and sexual signals, so that sexual selection has apparently contributed to interpopulation divergence in aposematic signals (Maan and Cummings 2009).

In butterflies, wing color patterns can serve sexual functions in inter- or intraspecific signaling or viability-related functions in aposematic signaling or mimicry. Selection for mimicry, which acts predominantly on females, seems to play a particularly important role in diversification of wing patterns (Kunte 2008). Interestingly, as in poison frogs, the same color patterns can serve both sexual and viability-related functions in butterflies, such that selection for novel mimicry in females can drive reproductive isolation (Jiggins et al. 2001, 2004). This suggests the possibility of conflict between sexual and viability selection (Estrada and Jiggins 2008). However, it also suggests that sexual selection could initiate the evolution of mimicry or aposematic signaling. Sexual selection could drive the evolution of color patterns that, by accident, enhance similarity to an unpalatable species (i.e., produce incipient mimicry), and viability selection may then enhance the mimicry. Consistent with this possibility, comparative analysis shows frequent gains of ancestrally male-limited ornaments by females in some butterfly genera (Oliver and Monteiro 2011).

Body Size and Shape

Body size and shape play important roles in both sexual competition and ecological strategies in many animals. Thus, ecological co-optation could play an important role in the evolution of viability-enhancing adaptations involving these traits.

Body size influences virtually all aspects of physiology, life history, and resource use, but it also affects male combat performance and social dominance in many species (Blanckenhorn 2000; Drovetski et al. 2006; Chown and Gaston 2010). Sexual selection can drive massive changes in body size, affecting both mean size and sexual size dimorphism (Maynard Smith 1978; Blanckenhorn 2005), and it could therefore play a major role in the long-term evolution of body size (West-Eberhard 2003). This suggests that evolution of body size via sexual selection could influence many aspects of the ecological strategy, such as dietary preferences and requirements, vulnerability to predators, tolerance for ambient conditions such as temperature and humidity, and mean life span, and open up new niches. An interesting potential example of this process is provided by the mammals, in which there has been a long-term evolutionary trend of increasing mean body size (Cope's rule), along with a diversification of ecological strategies. Analysis of existing mammalian communities suggests that long-term evolution of increased body size cannot be attributed to viability-related advantages of larger size (Damuth 1993). Instead, evolution of large body size in mammals may have been driven by sexual selection on males (McLain 1993). Along the way, repeated ecological co-optation of large body size could have contributed to ecological diversification.

In many animals, appendages such as legs, antennae, and mouthparts function in male-male or male-female sexual interactions (Kawano 1997; Sivinski 1997; Emlen and Nijhout 2000; Bonduriansky 2003; Puniamoorthy et al. 2008), but these structures typically also retain their primitive viability-related roles as locomotory, sensory, and feeding traits. Modification of such structures in response to sexual selection may therefore have direct implications for their viability-related function (e.g., locomotory efficiency on different substrates, olfactory acuity, or ability to exploit different foods). Interestingly, elongated legs and antennae occur as male-limited secondary sexual traits in some insect species but as sexually monomorphic traits in other species (McAlpine 1987), suggesting a possible role for ecological co-optation in the evolution of these traits.

A particularly interesting potential example of ecological co-optation is provided by the evolution of body shape in brood-parasitic sweat bees (Halictidae). In this group, females exhibit many morphological characters that typify

males in pollen-collecting species, such as the absence of structures required for pollen collecting. It has been suggested that this suite of characters evolved in sweat bees through cross-sexual transfer of male morphological characters (Wcislo 1999). The male body shape characteristic of pollen-collecting bee species, which presumably evolved through sexual selection, may therefore have been co-opted for a brood-parasitic lifestyle by female sweat bees.

Many lizards exhibit striking sexual dimorphism in body size and shape. In some groups, dimorphism is thought to evolve as an ecological strategy (competitive displacement) driven by intraspecific competition over resources (Butler et al. 2000, 2007; Butler and Losos 2002; Pincheira-Donoso et al. 2009). However, because some of the same traits that are associated with competitive displacement are also under sexual selection in male lizards (Trivers 1976; Stamps et al. 1997; Cox et al. 2003), sexual selection on males could be responsible for initiating the evolution of distinct foraging strategies, as suggested by Slatkin (1984).

In addition, as with the color patterns of birds and butterflies, female lizards have, in some cases, acquired ancestrally male-limited "ornaments" such as gular sacs, rostral appendages, and dorsal crests (Ord and Stuart-Fox 2006). Although sexual selection on females is a potential explanation for female gains of such traits (Ord and Stuart-Fox 2006), these traits could also serve viability-related functions in females (e.g., in female-female competition over resources).

Sensory and Nervous Systems

Sense organs and brains are clearly important in both sexual and viability contexts. A potential example of the role of ecological co-optation in the evolution of visual systems is provided by the true flies (Diptera). In several dipteran families, sexual selection on males has driven the evolution of "holoptic" eyes that extend to the front of the head and merge or meet at the midline. In males, holoptic eyes typically occur in species where males engage in aerial pursuit of females (McAlpine 1987). For example, holoptic males of the bibionid fly *Plecia nearctica* swarm above female emergence sites and attempt to intercept females in flight (Hetrick 1970; Thornhill 1980). However, in some dipteran families (e.g., Culicidae, Synneuridae, Cecidomyiidae, Thaumaleidae, Ceratopogonidae, Sciaridae, Acroceridae, Nemestrinidae, Empididae, and Bombyliidae), holoptic eyes occur in females of some or all species (McAlpine 1987). Just as holoptic eye morphology enhances males' ability to detect and intercept females, holoptic eyes may also confer viability advantages—for example, by facilitating escape from aerial predators such as odonates—and such ecological advantages may have

favored the transfer of this trait to females in some lineages. Even in species with "dichoptic" (i.e., separate) eyes, the sexes may exhibit differences in eye size and shape that could reflect sexual selection on males (Holston and Nelson 2006). Likewise, other sensory adaptations that evolve to function in mate searching or assessment, such as specialized hearing or chemoreception mechanisms (see below), could also be co-opted for viability-related roles.

Specialized brain structures and neural processing capabilities have evolved in many lineages to serve in courtship signaling or mate assessment. For example, in many bird species, males possess specialized brain regions that function in the learning and production of songs or visual displays used in courtship or male-male signaling, and females possess specialized neural circuitry that functions in the assessment of male courtship signals (Székely et al. 1996; Leitner and Catchpole 2002; DeVoogd 2004; Day et al. 2005; Gil et al. 2006). An enlarged brain or specialized neural circuitry that evolves in a sexual context could be co-opted for viability-related functions. Indeed, there is evidence that brain size and intelligence are related to ecological flexibility and success in birds and other animals (Sherry 2006; Morand-Ferron et al. 2007; Shumway 2008). It has also been suggested that the coevolution of mate preferences and sexual display could have driven the expansion of the human brain and the evolution of unique human mental capabilities such as language and creativity, which were subsequently co-opted for viability-related functions (Miller 1994, 2001; Miller and Todd 1995).

Cuticular Hydrocarbons

The cuticular hydrocarbons (CHCs), a blend of waxy compounds coating the cuticle of insects and many other arthropods, probably originated as a defense against desiccation but have acquired sexual signaling functions in many groups (Singer 1998). For example, in several species of *Drosophila*, the CHCs confer protection against desiccation (Gibbs 1998; Rourke and Gibbs 1999; Kwan and Rundle 2010) while also serving as an important sexual signal for both sexes (Chenoweth and Blows 2003, 2005; Friberg 2006; Skroblin and Blows 2006; Chenoweth et al. 2008; Arienti et al. 2010). Studies suggest that ecological factors can influence the evolution of CHC blend (Etges and Ahrens 2001) as well as the importance of component CHCs in mate choice (Herzner et al. 2005; Rundle et al. 2005, 2009) and thus play a role in the evolution and maintenance of reproductive isolation through mate choice (Stennett and Etges 1997; Higgie et al. 2000; Etges and Ahrens 2001). Conversely, changes in CHC blend brought about by sexual selection could affect the range of ambient conditions that insects can tolerate and the resources that they can exploit. Sexually selected CHC phe-

notypes could thus be co-opted for viability-related functions. The role of ecological co-optation in CHC evolution can be clarified by exploring the genetic basis of CHC expression in both sexes (e.g., see Liimatainen and Jallon 2007; Chenoweth and Blows 2008; Gleason et al. 2009) and by examining the roles of sexual and viability-related functions in CHC evolution within a phylogenetic framework.

Silk Production in Spiders

The silk-producing glands (spinnerets) of spiders, which play a key role in the ecological innovation of web-based predation and dispersal, appear to have originated as reproductive traits. Spinnerets are located in the genital region, and silk is used for the construction of sperm webs and egg sacs in all spiders, whereas the construction of webs for foraging or dispersal has a more limited phylogenetic distribution (Craig 1997). Thus, it is possible that silk production originally evolved for a sexual purpose (sperm web production) and subsequently underwent ecological co-optation for foraging and dispersal in both sexes (see Schultz 1987; West-Eberhard 2003).

Conclusions

Theory and evidence suggest that sexual selection and conflict could potentially play a direct role in ecological diversification. Because sexual selection and conflict can readily displace populations from their viability optima, sexual coevolution can, in principle, allow populations to explore a wide phenotypic space. Some sexual traits could then serve as preadaptations for novel viability-related functions, and such traits could be transferred between sexes. Thus, modifications to the phenotype that occur in a sexual context could be co-opted as novel strategies for exploitation of the current niche or a new niche. Through this process, the diversifying power of sexual selection and conflict could be harnessed to generate ecological diversity.

The examples adduced above suggest that ecological co-optation is a plausible evolutionary hypothesis for a variety of ecological traits. As these examples illustrate, many structures, organs, and appendages serve a combination of sexual and ecological functions. Ecological co-optation could readily play a role in the evolution of such traits because adaptation in one functional context can have direct consequences in the other functional context: a phenotypic modification in response to sexual selection can serve as a preadaptation for a novel viability-related role. In the most general sense, sexual selection can drive the evolution of whole-organism performance and the acuity of sensory and neural systems (see Rowe and Houle 1996; Murphy 1998; Lailvaux and Irschick 2006). Therefore, in-

cipient stages in the evolution of many complex adaptations, such as eyes, brains, and locomotory systems, could be driven by either sexual or viability selection, and their long-term evolution could involve repeated episodes of ecological and sexual co-optation.

By facilitating the evolution of niche polymorphisms, ecological co-optation may promote population splitting and speciation (see Coyne and Orr 2004). However, population splitting is not an inevitable corollary of niche polymorphism: the outcome in any particular case will depend on whether reproductive isolation is established between incipient host races or ecotypes (see Coyne and Orr 2004). Because the initial stage of ecological co-optation involves sexual selection and conflict within a population, any eventual split in the population will begin under sympatry. Although sympatric speciation presents considerable theoretical difficulties (Bolnick and Fitzpatrick 2007), sexual selection and conflict could facilitate this process (Lande and Kirkpatrick 1988; Gavrilets 2000). Interbreeding between new ecotypes may be opposed, for example, by a combination of divergent female mating preferences and reduced viability of hybrids (Lande and Kirkpatrick 1988). A number of factors may therefore combine to determine whether or not population splitting and speciation occur, including the rate of gene flow, the genetic architecture of key traits, the strength of disruptive selection, and perhaps the number of ecologically important traits that are selected differently in the original and novel niches (Coyne and Orr 2004; Nosil and Harmon 2009; Nosil et al. 2009).

Alongside other ideas (fig. 2), the ecological-co-optation hypothesis illustrates how the within-population dynamics of sexual selection and conflict could influence the population-level processes of ecological adaptation and diversification. The fitness landscape on which sexual populations evolve can be viewed as the combination of a common "viability landscape" of ecological adaptation and sex-specific selection vectors such as sexual and sexually antagonistic selection (see Lande and Kirkpatrick 1988). Sexual-selection vectors are evidently prone to rapid and arbitrarily change (see Miller and Todd 1993; Iwasa and Pomiankowski 1995; Holland and Rice 1998; Gavrilets 2000; Boughman 2001, 2002; Gavrilets et al. 2001; Jiggins et al. 2001, 2004; Gavrilets and Hayashi 2006), and they can generate complex, unpredictable evolutionary dynamics (see Iwasa and Pomiankowski 1995; Gavrilets 2000; Gavrilets and Hayashi 2006). The dynamics of sexual coevolution can therefore be likened to deterministic chaos, where a small perturbation can lead to major change (Ferrière and Fox 1996). Thus, whereas the topography of the viability landscape may be relatively stable, the chaotic dynamics of sexual coevolution may engender a (net) fitness landscape that is unstable and unpredictable (see Mil-

ler and Todd 1993). On such a landscape, sexual selection and conflict could furnish the "trial and error mechanism on a grand scale" sought by Wright (1932).

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A pair of mating neriid flies (*Telostylinus angusticollis*), illustrating the male's strikingly elongated legs. Photograph by R. Bonduriansky.