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Understanding the Evolution of Ecological Sex Differences: Integrating Character Displacement and the Darwin-Bateman Paradigm

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Abstract

Sex differences in selection arise for two possible reasons: 1) differences originating from anisogamy – the Darwin-Bateman paradigm – and 2) competition-driven ecological character displacement (ECD), agnostic of anisogamy. Despite mounting evidence of ECD and increasing focus on the ecological causes and consequences of sexual dimorphism, progress in understanding the evolution of ecological sex differences has likely been hindered because ecological dimorphisms are not exclusive to ECD. I argue that embracing non-exclusivity of causal models of sexual dimorphism itself provides insights into evolution of sex differences. This integrated view of the evolution of sexual dimorphism leads to four predictions for how sex-specific selection and phenotypic divergence between the sexes change over the course of the evolution of sexual dimorphism. First, dimorphism resulting directly from anisogamy likely precedes evolution of ecological dimorphism driven by ECD. Second, ecological sexual dimorphism driven by ECD may (initially) evolve in directions in trait space favored by other sources of sex-specific selection. Third, we may expect correlated evolution of ecological dimorphism and other forms of sexual dimorphism. Finally, ecological optima may be sex specific even when competition plays a role in reaching them. Rather than simply a less-parsimonious alternative explanation for ecological sex differences, ECD should be seen as one likely contributor to sex-specific selection that could act at predictable times during the evolution of ecological sexual dimorphisms.

Impact Statement

Sexual dimorphisms, or trait differences between males and females of the same species, represent a tremendous source of phenotypic diversity. Although often a clear outcome of differences in mating competition, in many other cases males and females have evolved differences in traits related to ecological niche, such as body size, resource and habitat use. Our understanding of how and why these ecological sexual dimorphisms evolve is unclear, yet critically important in light of emerging work highlighting the importance of ecology in mediating evolutionary conflicts between the sexes, the role of sex differences in eco-evolutionary dynamics, and the importance of competition as an evolutionary driver of phenotypic diversity. Typically, ecological sexual dimorphisms are thought to result either as a by-product of sexual selection and divergent gamete investment, or through competition-driven niche partitioning between the sexes (ecological character displacement) . In this paper I build upon past work to make the case that integrating both models of sexual dimorphism may be key to a complete understanding of how ecological sexual dimorphisms evolve. I review empirical evidence for character displacement between the sexes, finding many suggestive, but few concrete, examples. I go on to develop explicit predictions for the dynamics of female and male evolution under the hypothesis that both fundamental models of sexual dimorphism may act together to drive the evolution of sexual dimorphism. The general conclusion is that integrating classical ideas from evolutionary genetics and community ecology may often be necessary to fully understand the evolution of ecological differences between the sexes.

Paradigmatic views of sexual dimorphism

Striking differences between males and females of the same species are commonplace. To explain the evolutionary origins of these sexual dimorphisms, Darwin (Darwin 1871) proposed a special case of natural selection, sexual selection, and argued that fundamental differences in the reproductive interests of the sexes result in pervasive differences in the strength and direction of both sexual and natural selection in males and females. In modern parlance, Darwin's was the first causal explanation for why selection may be sexually-antagonistic (SA), which together with the relaxation of genetic constraints is a key feature of the evolution of sexual dimorphism (Bonduriansky and Chenoweth 2009, Cox and Calsbeek 2009). Darwin's arguments were later elaborated on and clarified by Bateman (1948), Trivers (1972), and many others since (Andersson 1994, Arnqvist and Rowe 2005, Parker 2014, Parker and Pizzari 2015). This work has resulted in a paradigmatic view of the evolution of sexual dimorphism rooted in anisogamy: the divergent gamete investment strategies that define the sexes set the stage for SA selection that drives the evolution of divergent degrees of mating competition, parental care, and other aspects of life history, leading to pervasive sex differences in selection that drive the evolution of sexual dimorphism (Figure 1A). This paradigm, known as the Darwin-Bateman paradigm (Parker 2014, Parker and Pizzari 2015), suggests anisogamy results in sex-specific optima, and consequentially pervasive SA selection and the evolution of sexual dimorphism, for shared traits. Although the Darwin-Bateman paradigm has been challenged (Gowaty and Hubbell 2009, Ah-King 2013), these models invoke chance or assumed life history differences between the sexes (presumably arising from anisogamy) and so it is unclear whether they constitute a general alternative explanation for the evolution of sex differences (Shärer et al. 2012 , Kokko et al. 2013). Under the Darwin-Bateman paradigm, which has substantial support in nature (Kokko et al. 2013, Janicke et al. 2018), anisogamy is the ultimate evolutionary cause of SA selection and all resulting sexual dimorphisms (Shärer et al. 2012).

Only one plausible alternative adaptive causal explanation for the evolution of sex differences exists, and its explanatory power is limited to cases of sexual dimorphism in traits such as feeding morphology, size, and habitat use (henceforth 'ecological' sexual dimorphisms). This is a model of resource competition driven ecological character displacement (ECD) between the sexes, and conceptually parallels models of interspecific ECD. In this model frequency and density dependent competition for a shared resource generates SA selection on resource acquisition traits and thus drives the evolution of ecological sexual dimorphism (Slatkin 1984, Bolnick and Doebeli 2003, Cooper et al. 2011). ECD is unique in that as a process it ignores gamete dimorphism and any consequential divergence in life history, requiring the sexes to exist only in name; we could be describing divergent selection and displacement between any two morphs or isogamous mating types whose quantitative traits are imperfectly genetically correlated. This model is thus logically distinct from the Darwin-Bateman paradigm, for the two general models differ fundamentally in their explicit and implicit incorporation of anisogamy and life history divergence between the sexes (Figure 1B). This distinction has non-trivial consequences for understanding when and why SA selection resulting from ECD may act to drive the evolution of sexual dimorphism, and has likely shaped the history of research on ECD itself.

Here, I make the case that ECD between the sexes is most likely to act in conjunction with SA selection and morphological divergence arising from the Darwin-Bateman paradigm. Although this point has been suggested at various points in the past (Selander 1966, Power 1980, Hedrick and Temeles 1989, De Lisle and Rowe 2015a), recent advances in sexual conflict research highlight a need for more explicit integration of ecological causes of sexual dimorphism within the Darwin-Bateman paradigm. I suggest that rather than an obstacle to our understanding of the evolution of sex differences and SA selection, integrating ECD with existing ideas of the Darwin-Bateman paradigm leads to testable predictions for the dynamics of SA selection, male and female coevolution, and the evolution of sexual dimorphism. Embracing both paradigmatic causal models of SA selection might often be necessary for a complete understanding of how and why ecological sex differences evolve.

Integrating ECD within the Darwin-Bateman Paradigm

Despite the substantial body of work discussed above and the prevalence of ecological sexual dimorphisms in nature (Shine 1989), the evolution of ecological differences between the sexes and more generally the role that the ecological environment plays in mediating sexual conflict, presents a distinct and unresolved challenge (Connalon et al. 2018). Both paradigmatic models can drive the evolution of ecological sexual dimorphisms, and, as has been pointed out before (Selander 1966, Slatkin 1984, Hedrick and Temeles 1989, Shine 1989), both models could jointly contribute to SA selection and the evolution of a given sexual dimorphism. This has led to claims that ECD between the sexes is impossible to test directly, and the Darwin-Bateman paradigm is a more parsimonious explanation for SA selection and the evolution of sex differences regardless (Shine 1989); concomitantly, a renaissance of work aimed at understanding interspecific ECD has largely ignored intraspecific ECD between the sexes (Pfennig and Pfennig 2012, Stuart and Losos 2013, Germain et al. 2018). Yet, recent work (De Lisle and Rowe 2015a) has shown that, similar to interspecific ECD, direct tests of the hypothesis of ECD between the sexes are difficult but tractable (See **Box 1**). Despite mounting indirect evidence of an important role for competition in the evolution of sexual dimorphism, direct evidence is rare, in part because few studies have attempted to link competition with sex-specific fitness variance (**Box 2**). Added to this are a growing number of theoretical and empirical studies indicating ecological factors and sexual selection can interact to affect total SA selection and the position of sex-specific optima, the expression of sexual antagonism, and consequentially the evolution of sexual dimorphism (Arbuthnott et al. 2014, Camus et al. 2017, Perry et al. 2017, Zajitschek and Connallon 2017, Connalon et al. 2018, De Lisle et al. 2018a, Yun et al. 2018). Concomitantly, a number of recent studies have highlighted the potential contribution of sexual dimorphism and SA selection to community dynamics (Giery and Layman 2019, Svensson 2019, Fryxell et al. in press). This body of work together suggests that a complete understanding of the evolutionary origins and ecological consequences of sexual dimorphism may often require explicit consideration of the multiple factors influencing sexually antagonistic selection.

Three lines of evidence suggest the evolution of ecological character displacement between the sexes might be best understood by integration with the Darwin-Bateman paradigm of evolution of sexual dimorphism, rather than viewed as a separate and alternative process (e.g. Figure 1B). First, many theoretical models and much empirical data indicate that sex differences in optimal mating rate and parental investment that drive SA selection are a direct outcome of the gamete dimorphism that defines males and females (but see Ah-King 2013), and thus initial phenotypic divergence between the sexes seems most likely to arise due to the evolution of divergent reproductive strategies (Shärer et al. 2012 , Lehtonen et al. 2013); that is, the ancestral stages of the evolution of sex differences seem almost certain to evolve as illustrated in Figure 1A.

Second, character displacement theory makes clear statements for how the strength of competition-driven selection should change over the course of phenotypic divergence between competing lineages (Doebeli 1996, Schluter 2000b). Divergent natural selection is weak during the early stages of character displacement, despite high competition. This is because competition (and selection) are both frequency and density dependent; when both populations (or sexes) are in complete overlap, change in fitness per unit change in phenotype is weak because all phenotypes are at high frequency (Schluter 2000b). As lineages (or sexes) begin to diverge in mean phenotype, the strength of selection increases because extreme phenotypes are now further from the grand mean, and have a high fitness advantage over those closer to the mean (Schluter 2000b, De Lisle and Rowe 2015a). This effect creates a pattern wherein divergent selection is strongest after phenotypic means have already begun to diverge.

Third, the above argument is based on partitioning of a continuously distributed (Gaussian) resource axis; that is, in the absence of competition, selection is stabilizing towards the most abundant resource value (Slatkin 1984, Bolnick and Doebeli 2003, Rueffler et al. 2006). Yet sexual selection and SA natural selection resulting directly from anisogamy can create ecological optima that are not equal for the sexes (Maklakov et al. 2008, Reddiex et al. 2013), a case analogous to Slatkin's (1984) 'dimorphic niches' model, with competition then coming into play to accelerate evolution towards these optima. For example, sex-specific nutritional optima can be determined in part by the energy requirements associated with female and male reproductive roles (e.g., Belovksy 1978), yet these divergent optima do not exclude the possibility that competition affects the dynamics of selection during ecological divergence.

Predictions of the integrated view of ecological sexual dimorphism

The above lines of reasoning suggest that if and when it occurs, SA selection arising from ECD between the sexes seems most likely to act in concert with other causes of SA selection, rather than as a sole explanation for the evolution of sexual dimorphism. In this view, resource competition-driven SA natural selection arises as an indirect outcome of anisogamy, and could serve to accelerate the evolution of sexual dimorphism or change the position of male and female optima at equilibrium (Hedrick and Temeles 1989), suggesting that a complete understanding of the evolution of ecological sex differences may require explicitly embracing these multiple interacting mechanisms. Although others have recognized that ECD and the Darwin-Bateman paradigm are not mutually-exclusive casual explanations for SA selection (Hedrick and Temeles 1989, Shine 1989, De Lisle and Rowe 2015a), we can expand this integrated view to generate predictions for the correlated evolution of the divergent female and male life histories, ecological character displacement, and niche divergence between males and females.

Prediction 1: SA selection from anisogamy precedes the action of ECD

First, sex differences in sexual and natural selection arising directly from anisogamy act to drive the initial stages of the evolution of sexual dimorphism, with frequency-dependent resource competition acting at intermediate stages (degree of morphological divergence) to affect total SA selection (Figure 1C, Figure 2). That is, ECD is predicted to contribute to SA selection only after initial divergence between the sexes driven by SA selection resulting directly from anisogamy. We expect under the Darwin-Bateman paradigm for anisogamy to drive SA selection on a multivariate suite of traits related to male and female fitness. This initial evolution of sexual dimorphism driven by anisogamy would be expected to create conditions favorable to the action of ECD under two conditions. First, if the traits that are initial targets of SA selection are related to resource acquisition or genetically correlated to resource acquisition. Second, the evolution of sexual dimorphism in display or reproductive traits unrelated to resource acquisition could nonetheless lead to divergent nutritional demands in males and females (Maklakov et al. 2008), in which case initial evolution of sexual dimorphism in resource use traits would be driven by SA selection arising directly from anisogamy. Note that this prediction applies to the early stages of *morphological divergence* in ecologically-important traits, rather than the timescale over which divergence has evolved (e.g., Schluter 2000b).

This prediction could be tested or falsified by functional analysis of ecological sex differences in the early stages of the evolution of ecological sexual dimorphism, because the expectation is that these initial ecological sex differences are in fact targets of selection directly related to divergent reproductive strategies or are genetically correlated to traits that are. In some cases this prediction may leave testable signatures at the genomic level; under some conditions (e.g., arms race dynamics) divergent sexual selection may leave a signature of selective sweep(s) (Rowe et al. 2018), which may be followed by balancing selection when the traits under selection experience negative-frequency dependence characterizing the process of ECD. A difficulty of testing this prediction (especially with genomic data) is that SA natural selection, besides that arising from resource competition, may nonetheless act to drive the early stages of the evolution of sexual dimorphism. Data suggest that SA selection under the Darwin-Bateman paradigm can manifest as differential survival (Chen and Kirkpatrick 2016), and population genetic theory makes little distinction between potential causes of SA selection (Kidwell et al. 1977, Connallon and Clark 2014).

Prediction 2: Alignment between drivers of SA selection

Prediction 1 implies a second (and perhaps transient) prediction, that SA selection from resource competition, and thus the evolution of ecological sexual dimorphism, should initiate in directions through trait space favored by other sources of SA selection (Figure 2). That is, we might expect some alignment between alternative sources of SA selection in the early stages of the evolution of ecological sexual dimorphism. As the sexes diverge in response to sex-specific selection arising in the Darwin-Bateman paradigm, Prediction 1 implies that competition would be expected to increase the strength of selection acting in this initial direction of divergence if resource competition is frequency dependent. Again, because this prediction arises from competition theory on the expected strength of selection during character displacement, it applies to early/intermediate stages of *morphological divergence* between the sexes, rather than the timescale over which dimorphism has evolved. Evolution of sexual dimorphism under aligned competition induced SA selection and other sources of SA selection (e.g., sexual or fecundity selection) may nonetheless be halted by countervailing natural selection (such as predation) or genetic constraints.

This prediction could be tested using phenotypic selection studies of wild populations where the geometry of fitness surfaces estimated on the same traits but using different fitness components are compared (Chenoweth et al. 2012), with predicted alignment of the fitness surface estimated for mating success with the fitness surface estimated for a relevant natural fitness component (e.g., growth rate, survival). The strength of this alignment could be compared across traits or directions through trait space differing in their degree of sexual dimorphism.

Alternatively, in some systems, it may be possible to estimate total SA selection in the presence and absence of resource competition. Such a manipulation would allow the comparison of both the strength and direction of total SA selection and SA selection in the absence of competition.

Prediction 3: Correlated evolution of 'ecological' dimorphism and other forms of sexual dimorphism

If ecological sexual dimorphism driven by ECD follows the evolution of sexual dimorphism arising from other causes, then we might expect a positive correlation in the extent of ecological divergence between the sexes and total (e.g., including sexually selected display traits) multivariate sexual dimorphism. It is certainly true that sexual dimorphisms in many or most display traits can be completely unrelated to resource use. However, multivariate character displacement theory suggests that as the dimensionality of selection (in this case sex-specific selection) increases, the likelihood of competitive displacement occurring along at least one dimension increases (Svardal et al. 2014). That is, although the magnitude of sexual dimorphism in any one dimension might be irrelevant for the occurrence of ECD if that dimension is not associated with resource use, as the dimensionality and extent of multivariate sexual dimorphism increases, so to does the probable importance for a role for competition to drive the evolution of further sexual dimorphism in at least one dimension of phenotype space.

This prediction could be tested using comparative methods and data on sex differences in display and ecological traits. For example, data on diet or habitat use could be combined with measures of morphological dimorphism in traits clearly under SA selection related to anisogamy (such as display or other mating related traits), with the prediction of correlated divergence across lineages. Such an approach was taken by Stamps et al. (Stamps et al. 1997), although they found evidence refuting this prediction in *Anolis* lizards. Experimental evolution provides another approach, where the strength of sexual selection could be elevated and resource-use divergence compared to control populations after a suitable number of generations; many such mating system manipulations have been performed in experimental evolution designs, although none have investigated the possibility of correlated ecological divergence to my knowledge.

Prediction 4: Realized niches will be sex specific; Parallel evolution of ecological dimorphism

Finally, this integrated view suggests that in the later stages of sexual dimorphism, niche divergence between the sexes will be sex specific (e.g. De Lisle and Rowe 2015b). That is, because under this integrated view the evolution of ecological sexual dimorphism driven by ECD is initiated only after the action of SA selection directly related to the anisogamy, female and male ecological optima will differ in the late stages of the evolution of dimorphism, and so male and female 'niches' are not interchangeable. Put another way, the integrated view suggests that at equilibrium separate ecological peaks for males and females are separated by an untraversable fitness valley maintained in part by divergent reproductive strategies that result from anisogamy (Figure 2). Prediction 4 has some empirical support. For example, in anoles (*Anolis spp.*) (Butler et al. 2007), stickleback (*Gasterosteus aculeatus*) (Cooper et al. 2011), walking stick insects (*Timema spp.*) (Roy et al. 2013), and salamanders (*Notophtalmus spp.*) (De Lisle and Rowe 2017), males and females occupy distinct regions of morphospace, suggesting macroevolutionary adaptive zones (and thus niches) are not equivalent for males and females of these varied groups.

This prediction can be tested by examining the sign of ecological divergence in female and male traits across lineages exhibiting independent transitions to ecological sexual dimorphism and similar mating systems. If sex-specific selection related to the anisogamy drives the initial stages of the evolution of sexual dimorphism, the direction (in trait space) of sex-specific ecological divergence should be consistent across lineages. That is, evolution of ecological sexual dimorphism is expected to be parallel across related lineages under prediction 4. Although a large literature on parallel, or convergent, evolution exists, this literature has rarely considered ecological sex differences (Oke et al. 2018), and large-scale metanalysis of the parallelism of sexual dimorphism would be useful. Other, more direct tests of prediction 4 may in some cases be possible. In some systems, ‘transplant’ experiments may be possible, where male and female fitness is estimated under environmental conditions typical of each sex (e.g., De Lisle et al. 2018b).

Note that prediction 4 is not unique to the action of ECD. SA natural selection that arises purely from anisogamy-related differences in reproductive interests are expected to lead to the evolution of sex-specific niches even in the absence of resource competition. However, because ECD alone (Figure 1b) predicts that the sign of phenotypic divergence between males and females should be random, patterns consistent with this prediction allow the hypothesis of ‘pure ECD’ to be rejected. Moreover, and more importantly, conceptual and mathematical models relating ecological dimorphism to community assembly and diversification (Bolnick and Doebeli 2003, Butler et al. 2007) assume implicitly that niches are interchangeable across the sexes. Yet even if ECD is a critical contributor to SA selection, the integrated view nonetheless predicts patterns of ecological sexual dimorphism will often be consistent across related lineages.

These four predictions are not proposed as a test of the action of resource-competition driven SA selection/ECD between the sexes. Such tests are possible and described in Box 1,

Figure 2, and could nonetheless be conducted in conjunction with tests of prediction 2 above. Rather, these predictions reflect patterns that seem likely to occur if both paradigmatic causes of SA selection together shape the evolution of ecological sex differences. In the absence of ECD, SA selection resulting from anisogamy may be expected to influence niche evolution in other ways; for example, allowing for the co-option of previously sex-limited traits for the same novel ecological role in both sexes (Bonduriansky 2011). If frequency-dependent resource competition contributes to SA selection and the evolution of sexual dimorphism, we expect it do so in a predictable way, and consideration of this may be useful when attempting to understand the ecological and evolutionary causes and consequences of sex differences.

Conclusions and future directions

Existing evidence makes the general importance of resource competition as a driver of SA selection and sexual dimorphism difficult to determine. The large number of suggestive cases of ecological sexual dimorphisms across a range of animal and plant taxa (Box 2) is, by itself, enough to indicate that establishing the prevalence of ECD between the sexes as an important open question for our understanding of adaptation in dioecious organisms. Very few studies have assessed the contribution of resource competition to sex-specific fitness variance directly. This relative paucity of direct empirical attention to the hypothesis of ECD is probably due, to some extent, to the inherent difficulty of direct tests of the hypothesis of ECD (Box 1). Yet this paucity also likely reflects a prevailing view that in its agnosticism towards the anisogamy, the hypothesis of ECD lacks parsimony (Shine 1989) and the fact that most studies of sexual antagonism and SA selection have justifiably focused on conflicts arising directly from divergent gamete investment. Yet rather than an unlikely alternative explanation for the evolution of ecological sexual dimorphism, resource competition is a likely contributor to SA selection that is expected to act at predictable times within the Darwin-Bateman paradigm, leading to many outstanding questions on the evolution of sex differences and their consequences (see **Box 3**). Direct tests of competition's role in the evolution of sexual dimorphism are tractable, although rather than pitting sexual selection, divergent mating strategies typical of the sexes, and ecological causes against each other as alternative causal explanations, they should be viewed and studied as potentially-interacting forces that could jointly shape the evolution of sexual dimorphism.

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BOX 1. Testing the hypothesis of Ecological Character Displacement between the Sexes

Past workers have suggested a number of approaches for testing the hypothesis of ECD between the sexes, ranging from simple morphometric analysis of ecological sex differences (Shine 1989), to phenotypic selection analyses (Price 1984, Hedrick and Temeles 1989), to manipulative experiments (De Lisle and Rowe 2015a). Yet like tests of the hypothesis of interspecific ECD, any single empirical approach is unlikely to provide compelling evidence on its own. More recently, De Lisle and Rowe (De Lisle and Rowe 2015a) attempted to define a set of four minimal criteria for an empirical demonstration of divergent ecological character displacement between the sexes. These criteria reproduced in Table I. Demonstration that the sexes have diverged in ecologically important (Criterion I) heritable (Criterion II) traits and that resource competition limits individual fitness (Criterion III) satisfies the requirement, for demonstration of ECD, that reduced competition increases fitness and that the sexes have begun to diverge in ecologically-relevant traits. Even in light of such evidence, a true test of ECD between the sexes requires a demonstration that divergence in morphology reduces the strength of competition between the sexes (Criterion IV). Correlations between proxies for the strength of competition and the expression of sexual dimorphism across populations in the wild ((e.g. Pincheira-Donoso et al. 2018)) is a common form of evidence for Criterion IV, although many alternative explanations for such a pattern exist. A more powerful approach is the statistical comparison of fitness surfaces, estimated using a fitness proxy that captures individual resource acquisition, across experimental units differing in the strength of competition and the distribution of ecological phenotypes (Bolnick and Lau 2008, De Lisle and Rowe 2015a, De Lisle and Svensson 2017). Such an approach expands on traditional phenotypic selection analyses, advocated in the past for tests of ECD between the sexes (Hedrick and Temeles 1989), in a major way because it allows identification of resource competition as a causal agent of selection and simultaneously tests the prediction from competition theory that selection is frequency- and density-dependent (Slatkin 1984) (see also Figure 2). For example, in a comparative study of stickleback populations (*Gasterosteus aculeatus*), Bolnick and Lau (Bolnick and Lau 2008) showed a reduction in strength of divergent selection in lakes with elevated levels of multivariate sexual dimorphism. Major caveats of tests employing comparative selection analyses is that they can only be employed when the distribution of female and male phenotypes overlap (De Lisle and Rowe 2015a), and they invite a number of complex statistical and methodological challenges (Chenoweth et al. 2012, De Lisle and Svensson 2017) on top of all the limitations of a traditional selection analysis, such as identification of appropriate measures of fitness and identification of the true targets of selection.

Box 1 Table I. Criteria for character displacement between the sexes

	Criterion	**Rationale**	**Potential empirical approaches**
I)	Sexes have diverged in resource use and morphology	Ecologically-relevant sexual dimorphism is a requisite	Morphometrics, mensurative studies of wild populations
II)	Morphological dimorphism has a genetic basis	Dimorphism, or more generally sex determination, must be genetic to qualify as 'character displacement'	Breeding experiments, pedigree analysis, genomics, phylogenetic history
III)	Competition limits, or did limit, female and male resource acquisition at the life stage at which dimorphism is expressed	Ecological sexual dimorphism cannot be the outcome of character displacement unless resource competition plays an important role in determining male and female fitness.	Experiments
IV)	Extent of competition can be linked to divergence along axis of morphological dimorphism	The strength of competition must be mediated by the traits that are sexually dimorphic	Experiments, carefully-designed comparative studies

BOX 2 Evidence of ECD Between the Sexes

A review of empirical papers citing Slatkin's (Slatkin 1984) formalization of ECD between the sexes indicates that strong evidence for ECD between the sexes is rare, although many studies provide some evidence suggestive of ECD (Table I; full details of literature search available in the Supplementary Material). Threespine stickleback (*Gasterosteus aculeatus*) present perhaps the most compelling case and the only one in which strong evidence for all four criteria exist, although they are not all presented in a single study; multiple independent studies present evidence for ecological dimorphism in heritable traits, and importantly, patterns of variation in divergent selection in the wild that are consistent with ECD and measured using identical female and male fitness components (Reimchen and Nosil 2001, Nosil and Reimchen 2005, Kitano et al. 2007, Bolnick and Lau 2008, Spoljaric and Reimchen 2008, Cooper et al. 2011). Resource competition has a demonstrated importance for individual fitness (summarized in Schluter 2000a). Eastern newts (*Notophthalmus viridescens*) provide a second example where multiple lines of experimental evidence for ECD between the sexes are available.

Many more studies reflect incomplete tests, where nonetheless the data and natural history suggest that a role for ECD could be quite likely. For example, a number of mensurative studies of bird foraging and morphology (particularly Piciforme woodpeckers and Passerines) suggest a possible role for ECD between the sexes. Perhaps the most exciting examples come from invertebrate animals and dioecious plants (e.g. , systems whose short generation times and/or experimental tractability make them conducive to explicit tests of the hypothesis. Plants, in particular, are especially amenable to experimental assessment of competition's role (or lack thereof) in generating sex-specific relationships between traits and fitness. Plants might also be more susceptible to resource competition-driven selection on morphological traits due to their sessile life history.

The conclusions of this survey are that: 1) there are very few clear examples of competition-driven ecological character displacement between the sexes, despite many potential cases, and 2) whether or not this reflects a lack of importance of the model cannot be ascertained without more direct studies that demonstrate or falsify patterns of sex-specific relationships between resource acquisition traits and fitness (Criterion IV; Box 1) predicted under a model of ECD.

Box 2 Table I. Studies with suggestive evidence of ECD between the sexes in animals and plants. Based on a review of published studies citing Slatkin 1984. Test = comparative (C), experimental (E), or a combination (C+E). A single asterisks indicates only circumstantial/weak or indirect evidence for a criterion. Double asterisks indicate some evidence of competition driving convergence.

Study	Species	Clade	Common name	Critera Met	Criteria Rejected	Trait(s)	Test
(Chazarreta et al. 2012)	*Campephilus magellanicus*	Piciformes	Magellanic woodpecker	I, IV*		diet, foraging strategy, bill size	C
(Wan et al. 2013)	*Rhinopithecus bieti*	Primates	Black snub-nosed monkey	I, IV*		foraging habitat use	C
(Martin and Pitocchelli 1991)	*Parus caeruleus*	Passeriformes	blue tit	I, IV*		body size, bill size	C
(De Lisle and Rowe 2017)	*Notophthalmus viridescens*	Caudata	eastern newt	I, IV*		size and head shape	C
(Queral-Regil and King 1998)	*Nerodia sipedon*	Squamata	Northern water snake	I, II		head shape, diet	E
(David et al. 2003)	*Drosophila melanogaster*	Diptera	fruit fly	I, II		body size	E
(Parsons et al. 2015)	*Labeotropheus fueleborni*	Perciformes	Fueleborn's ciclid	I, II		head shape	C+E
(Krause and Burghardt 2007)	*Thamnophis sirtalis*	Squamata	common garter snake	I, II		body and head size	C
(Foelker and	*Scolytinae*	Coleoptera	bark beetles	I, II		body size	E

Hofstetter 2014)							
(De Lisle and Rowe 2014)	*Notophthalmus viridescens*	Caudata	eastern newt	I, III		sex-specific responses to interspecific competition	E
(De Lisle and Rowe 2015a)	*Notophthalmus viridescens*	Caudata	eastern newt	I, III, IV		body size, head shape	E
(Spoljaric and Reimchen 2008)	*Gasterosteus aculeatus*	Gasterosteiformes	Threespine stickleback	I, IV*	II	multivariate morphology	C+E
(Butler et al. 2000)	*Anolis sp*	Squamata	anoles	I, IV*		multivariate morphology	C
(Dayan and Simberloff 1994)	*Mustela, Meles, spp.*	Mustelidae	weasels	I, IV*		skull size	C
(Dayan et al. 1990)	*Felis sp.*	Feliformia	cats	I, IV*		skull and tooth size	C
(Butler et al. 2007)	*Anolis sp*	Squamata	anoles	I, IV*		multivariate morphology	C
(Jones 1997)	*Darsyrus, Sarcophilus, Thylacinus*	Marsupialia	dasyurid marsupial	I, IV*		feeding morphology	C
(Pearson et al. 2002)	*Morelia spilota imbricata*	Squamata	carpet python	I, IV*		head shape, diet	C
(Shine et al. 2002)	*Laticauda colubrina, L. frontalis*	Squamata	sea krait	I, IV*		head size, body size, diet	C
(Kohorn 1994)	*Simmondsia chinensis*	Caryophyllales: Simmondsiaceae	goat nut	I, IV*		shoot morphology, habitat	C+E
(Bertiller et al. 2002)	*Poa ligularis*	Poales: Poaceae	grass	I, IV*		habitat use	C+E
(Nosil and Reimchen 2005)	*Gasterosteus aculeatus*	Gasterosteiformes	threespine stickleback	I, IV*		multivariate morphology	C
(Thom et al. 2004)	*Mustela vison*	Mustelidae	mink	I, IV*		tooth and skull morphology	C
(Levenson 1990)	*Tamias sp*	Rodentia	squirrels	I, IV*		body and head size	C

(Pasinelli 2000)	*Dendrocopos medius*	Piciformes	middle-spotted woodpecker	I, IV*	body and bill morphology, foraging habitat	C
(Summers et al. 1990)	*Calidris maritima*	Charadriiformes	Purple sandpiper	I, IV*	body size, diet	C
(Ebenman 1986)	*Parus major*	Passeriformes	great tit	I, IV*	bill size, tarsus size	C
(Kohorn 1995)	*Simmondsia chinensis*	Caryophyllales: Simmondsiaceae	goat nut	I, IV*	size, leaf morphology	C
(Kitano et al. 2012)	*Gasterosteus aculeatus*	Gasterosteiformes	threespine stickleback	I, IV*	multivariate morphology	C
(Viranta and Kauhala 2011)	*Vulpes vulpes*	Carnivora	red fox	I, IV*	skull size	C
(Cowley and Atchley 1988)	*Drosophila melanogaster*	Diptera	Fruit fly	I,II	feeding morphology	E
(Kitano et al. 2007)	*Gasterosteus aculeatus*	Gasterosteiformes	threespine stickleback	I,II	size and head shape	C+E
(Reimchen and Nosil 2004)	*Gasterosteus aculeatus*	Gasterosteiformes	threespine stickleback	I,II, IV	spine number, diet	C
(Leinonen et al. 2011)	*Gasterosteus aculeatus*	Gasterosteiformes	threespine stickleback	I,II, IV*	multivariate morphology	C+E
(Bedhomme et al. 2003)	*Aedes aegypti*	Diptera	Yellow fever mosquito	I,III	life history traits	E
(Simmons 1987)	*Gryllus bimaculatus*	Orthoptera	field cricket	I,III, IV*	body weight	E
(Fuselier and Mcletchie 2002)	*Marchantia inflexa*	Marchantiaceae	liverwort	I,III, IV**	pre-sexual life history	E
(Badyaev et al. 2001)	*Carpodacus mexicanus*	Passeriformes	house finch	I,IV	bill morphology	C
(Tibbetts and Safran 2009)	*Passeroidea*	Passeriformes	sparrows	IV*	plumage	C

(Maend et al. 2013)	*Ficedula hypoleuca*	Passeriformes	pied flycathcer	I, IV**	foraging strategy, diet	E
(Pincheira-Donoso et al. 2018)	*Liolaemus spp.*	Squamata	tree iguanas	I, IV	body size	C
(Duron et al. 2018)	*Campephilus magellanicus*	Piciformes	Magellanic woodpecker	I, IV*	foraging habitat use	C
(De Lisle et al. 2018b)	*Notphthalmus viridescens*	Caudata	eastern newt	III, IV*	size, head shape	E

Box 3 Outstanding Questions

1) How prevalent is ecological character displacement (ECD) between the sexes? Does resource competition play a general role in the evolution of ecological sexual dimorphisms? More direct tests are needed, that demonstrate or falsify a role for resource competition in generating sex-specific selection. The fact that the sexes share an evolutionary history in sympatry, coupled with the observation that intraspecific competition is often thought to be stronger than interspecific competition, suggests within-species ECD could be a more prevalent or general evolutionary process than interspecific ECD.
2) When it does occur, does ECD tend to drive further evolution of dimorphic traits that were already under sex-specific selection directly related to anisogamy and the Darwin-Bateman paradigm?
3) How might integrating competition models and sexual selection models change predictions for sexual dimorphism's role in higher level processes, such as: the evolution of reproductive isolation, ecological speciation, and extinction? Can we reconcile the sometimes-conflicting predictions of sexual dimorphism's role in diversification?
4) Emerging theory and data indicate that environmental variation plays a key role in mediating sex-specific selection and the expression of sexual antagonism (Connalon et al. 2018). One general conclusion from this work is that sexual antagonism is expected to be reduced in harsh environments or conditions of population maladaptation. How might resource competition act in these scenarios? Does ECD change these conclusions or amplify the expected patterns of variation in the importance of sexual antagonism?
5) Recent workers have highlighted an underappreciated but potentially important role for

sex-specific selection and sexual dimorphism, particularly resulting from sexual selection, in contributing to feedbacks between evolutionary change and ecological dynamics (Giery and Layman 2019, Svensson 2019, Fryxell et al. in press). This emerging work has not addressed in detail the potential role of ECD in generating such feedbacks. Yet in cases when resource competition acts jointly with other sources of sex-specific selection, it seems especially likely that the evolution of sexual dimorphism will have substantial ecological impact, and vice-versa; character displacement is itself the quintessential example of an 'eco-evo feedback'. Does incorporating the possibility that ECD and other sources of SA selection may act together change our understanding of sexual dimorphism's potential impact on ecological communities?

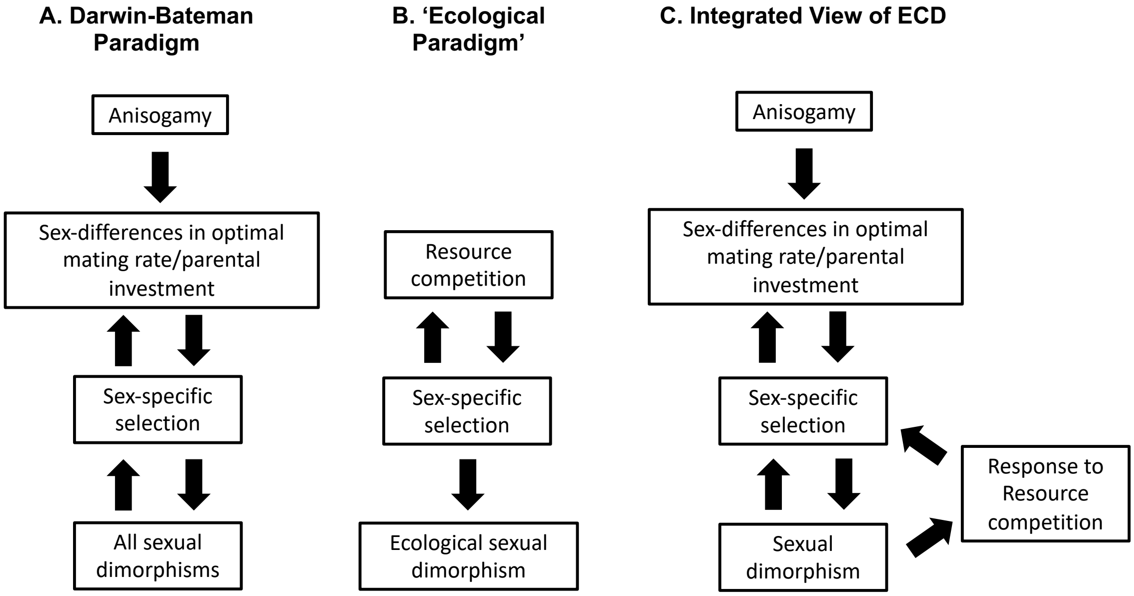

Figure 1. Foundational models of the evolution of sex differences. (A) represents the Darwin-Bateman paradigm of sexual dimorphism rooted in anisogamy. In this model, differential gamete investment that defines the sexes leads directly to sex differences in selection related to mating rate and parental investment, and thus the evolution of pervasive sex differences in life history. In this model, all pervasive sex differences in selection, sexual coevolution, and consequently all sexual dimorphisms are fundamentally rooted in anisogamy. (B) represents an alternative model of the evolution of sex differences: ecological character displacement (ECD). Resource competition drives divergent selection and the evolution of ecological dimorphism. Critically, this model makes no underlying assumptions regarding gamete investment, and so differs fundamentally from (A), although its explanatory power is limited to traits important for resource use. Although (A) and (B) differ fundamentally, they are not exclusive. When considered together, the mostly likely scenario for the evolution of sexual dimorphism is illustrated in (C). Under this integrated view, all sexual dimorphisms are ultimately rooted in anisogamy, although

ECD could have important consequences for the later stages of the evolution of sexual dimorphism. Feedback arrows between ECD, sexual dimorphism, and sex-specific selection indicate the frequency and density dependent nature of ECD; after extensive divergence competition-driven selection would be expected to relax.

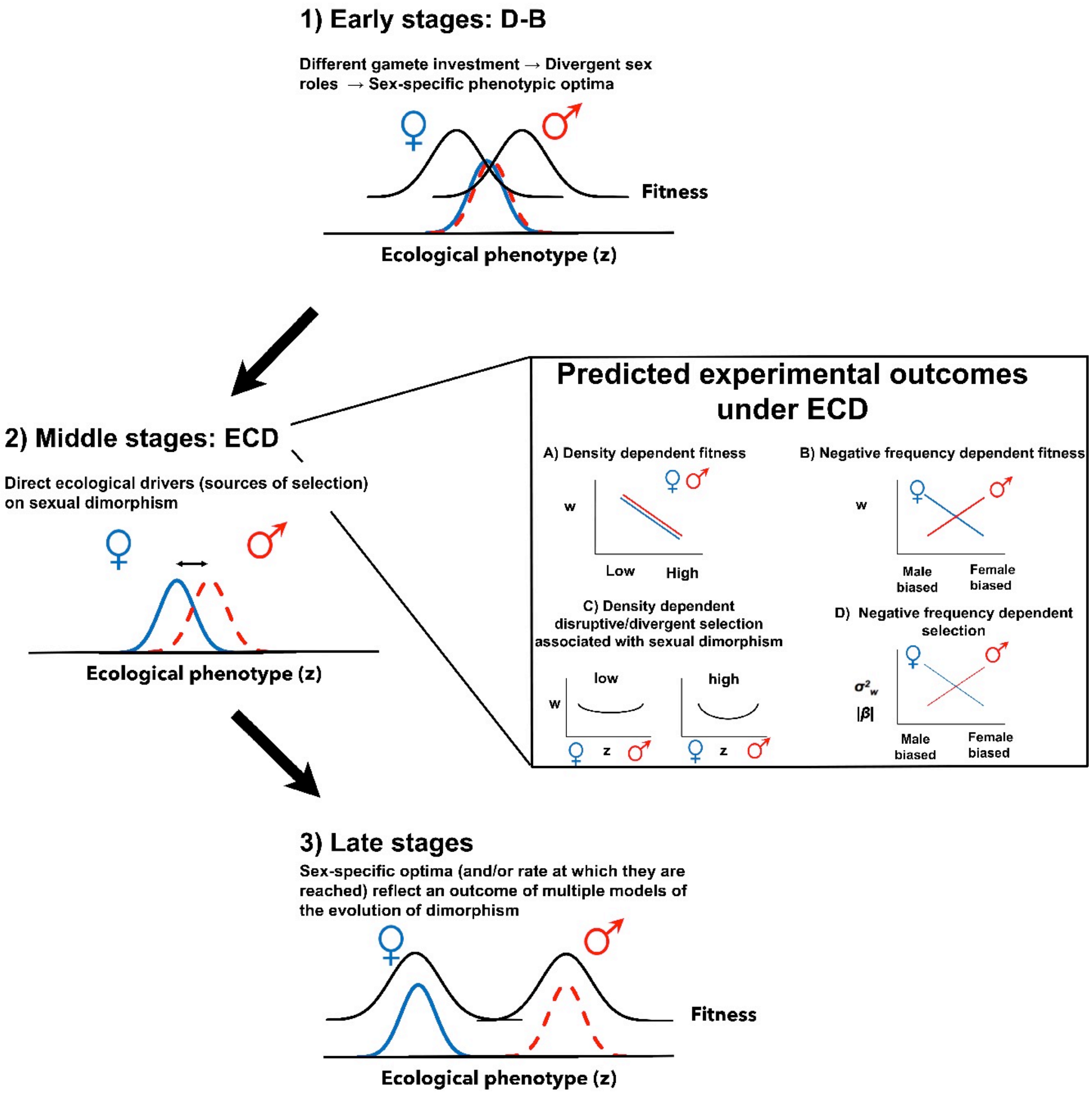

Figure 2. Conceptual illustration of how multiple causes of sex-specific selection act and interact to influence the evolution of sexual dimorphism. In the early stages of the evolution of sexual dimorphism (panel 1), the evolution of anisogamy leads to divergent male and female

life histories resulting in sex specific phenotypic optima, the Darwin-Bateman (D-B) paradigm. Following initial phenotypic divergence between the sexes, direct ecological drivers of sex-specific selection, ECD, step in to influence middle stages of the evolution of sexual dimorphism. For example, ecological character displacement could act at this stage to accelerate the evolution sexual dimorphism initiated by sexual selection. At this stage explicit predictions for experimental manipulations of density and phenotypic frequency (although within-sex frequency dependence is also expected, in the context of an experiment, sex ratio may often be the most logistically feasible way to manipulate the phenotypic distribution) can be made, at least for the case where female and male phenotypic distributions still overlap. First, we expect male and fitness or fitness components (e.g. growth or survival) to be negative density (A) and negative frequency (B) dependent. We also expect selection to be density and frequency dependent; males and females with extreme morphology should have a fitness advantage at high density (C), and in a frequency manipulation the strength of selection should be strongest for each sex when rare (D) (De Lisle and Rowe 2015a). Note that these predictions are specifically in the context of within-generation experimental perturbations aimed at uncovering the patterns of selection expected under resource competition-driven selection. Patterns opposite of any one of these expected outcomes would falsify the hypothesis that ECD is/has been acting to drive the evolution of sexual dimorphism. At the late stages of the evolution of sexual dimorphism (panel 3), male and female mean phenotypes will be located on adaptive peaks determined by multiple models of the evolution of sexual dimorphism.

REFERENCES

Ah-King, M. 2013. On anisogamy and the evolution of ‘‘sex-roles’’. Trends in Ecology and Evolution **28**:1-2.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, N.J.

Arbuthnott, D., E. M. Dutton, A. F. Agrawal, and H. D. Rundle. 2014. The ecology of sexual conflict: parallel evolution of male harm and female defense in experimental Drosophila melanogaster populations. Ecology Letters **17**:221-228.

Arnqvist, G., and L. Rowe. 2005. Sexual Conflict. Princeton University Press , Princeton NJ.

Badyaev, A. V., L. A. Whittingham, and G. E. Hill. 2001. The Evolution Of Sexual Size Dimorphism In The House Finch. III. Developmental Basis. Evolution **55**:176-189.

Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. Heredity **2**:349-368.

Bedhomme, S., P. Agnew, C. Sidobre, and Y. Michalakis. 2003. Sex-Specific Reaction Norms To Intraspecific Larval Competition In The Mosquito Aedes Aegypti. Journal of Evolutionary Biology **16**:721-730.

Belovksy, G. E. 1978. Diet optimization in a generalist herbivore: the moose. Theoretical Population Biology **14**:105-134.

Bertiller, M. B., C. L. Sain, A. J. Bisigato, F. R. Coronato, J. O. Aries, and P. Graff. 2002. Spatial Sex Segregation In The Dioecious Grass Poa Ligularis In Northern Patagonia: The Role Of Environmental Patchiness. Bioldiversity and Conservation **11**:69-84.

Bolnick, D. I., and M. Doebeli. 2003. Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. Evolution **57**:2433-2449.

Bolnick, D. I., and O. L. Lau. 2008. Predictable patterns of disruptive selection in three-spine stickleback. The American Naturalist **172**:1-11.

Bonduriansky, R. 2011. Sexual selection and sexual conflict as engines of ecological diversification. American Naturalist **178**:729-745.

Bonduriansky, R., and S. F. Chenoweth. 2009. Intralocus sexual conflict. Trends in Ecology & Evolution **24**:280-288.

Butler, M., S. A. Sawyer, and J. B. Losos. 2007. Sexual dimorphism and adaptive radiation in Anolis lizards Nature **447**:202-205.

Butler, M. A., T. W. Schoener, and J. B. Losos. 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean Anolis lizards. Evolution **54**:259-272.

Camus, M. F., K. Fowler, M. W. D. Piper, and M. Reuter. 2017. Sex and genotype effects on nutrient-dependent fitness landscapes in Drosophila melanogaster. Proceedings B **284**:20172237.

Chazarreta, L., V. Ojeda, and M. Lammertink. 2012. Morphological And Foraging Behavioral Differences Between Sexes Of The Magellanic Woodpecker (Campephilus Magellanicus). Ornitologia Neotropical **23**:529-544.

Chen, C., and M. Kirkpatrick. 2016. Sex-specific selectino and sex-biased gene expression in humans and flies. PLoS Genetics **12**:e1006170.

Chenoweth, S. F., J. Hunt, and H. D. Rundle. 2012. Analysing and comparing the geometry of individual fitness surfaces.*in* E. I. Svensson and R. Calsbeek, editors. The Adaptive Landscape in Evolutionary Biology. Oxford University Press, Oxford.

Connallon, T., and A. G. Clark. 2014. Evolutionary inevitability of sexual antagonism. Proceedings B **281**:20132123.

Connalon, T., F. Débarre, and X.-Y. Li. 2018. Linking local adaptation with the evolution of sex differences. Philosophical Transactions of The Royal Society B. **373**:20170414.

Cooper, I. A., R. T. Gilman, and J. W. Boughman. 2011. Sexual dimorphism and speciation on two ecological coins: patterns from nature and theoretical predictions. Evolution **65**:2553-2571.

Cowley, D. E., and W. R. Atchley. 1988. Quantitative Genetics Of Drosophila-Melanogaster .2. Heritabilities And Genetic Correlations Between Sexes For Head And Thorax Traits. Genetics **119**:421-433.

Cox, R. M., and R. Calsbeek. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. American Naturalist **173**:176-187.

Darwin, C. 1871. The descent of man and selection in relation to sex. J. Murray, London.

David, J., P. Gilbert, S. Mignon-Grasteau, H. Legout, G. Petavy, C. Beaumont, and B. Moreteau. 2003. Genetic Variability Of Sexual Size Dimorphism In A Natural Population Of Drosophila Melanogaster: An Isofemale-Line Approach. Journal of Genetics **82**:79-88.

Dayan, T., and D. Simberloff. 1994. Character displacement, sexual dimorphism, and morphological variation among british and irish mustelids. Ecology **75**:1063-1073.

Dayan, T., D. Simberloff, E. Tchernov, and Y. Yomtov. 1990. Feline Canines: Community-Wide Character Displacement Among The Small Cats Of Israel. The American Naturalist **136**:39-60.

De Lisle, S. P., D. Goedert, A. M. Reedy, and E. I. Svensson. 2018a. Climatic factors and species range positition predict sexually antagonistic selection across taxa. Philosophical Transactions of The Royal Society B. **373**:20170415.

De Lisle, S. P., S. Paiva, and L. Rowe. 2018b. Habitat partitioning during character displacement between the sexes. Biology Letters **14**:2018124.

De Lisle, S. P., and L. Rowe. 2014. Interactive effects of competition and social environment on the expression of sexual dimorphism. Journal of Evolutionary Biology **27**:1069-1077.

De Lisle, S. P., and L. Rowe. 2015a. Ecological character displacement between the sexes. The American Naturalist **186**:693-707.

De Lisle, S. P., and L. Rowe. 2015b. Independent evolution of the sexes promotes amphibian diversification. Proceedings of the Royal Society B: Biological Sciences **282**:20142213.

De Lisle, S. P., and L. Rowe. 2017. Disruptive natural selection predicts divergence between the sexes during adaptive radiation. Ecology and Evolution **2017**:1-12.

De Lisle, S. P., and E. I. Svensson. 2017. On the standardization of fitness and traits in comparative studies of phenotypic selection. Evolution **71**:2313-2326.

Doebeli, M. 1996. An explicit genetic model for ecological character displacement. Ecology **77**:510-520.

Duron, Q., J. E. Jimenez, P. M. Vergara, G. E. Soto, M. Lizama, and R. Rozzi. 2018 Intersexual segregation in foraging microhabitat use by Magellanic Woodpeckers (Campephilus magellanicus): Seasonal and habitat effects at the world's southernmost forests. Austral Ecology **43**:25-34.

Ebenman, B. 1986. Sexual Size Dimorphism In The Great Tit Parus-Major In Relation To The Number Of Coexisting Congeners. Oikos **47**:355-359.

Foelker, C. J., and R. W. Hofstetter. 2014. Heritability, Fecundity, And Sexual Size Dimorphism In Four Species Of Bark Beetles (Coleoptera: Curculionidae: Scolytinae). Annals of the Entomological Society of America **107**:143-151.

Fryxell, D. C., D. Weiler, M. T. Kinnison, and E. P. Palkovacs. in press. Eco-evolutionary dynamics of sexual dimorphism. Trends in Ecology and Evolution.

Fuselier, L., and N. Mcletchie. 2002. Maintenance Of Sexually Dimorphic Preadult Traits In Marchantia Inflexa (Marchantiacae). American Journal of Botany **89**:592-601.

Germain, R. M., J. Williams, D. Schluter, and A. Angert. 2018. Moving character displacement beyond characters using contemporary coexistence theory. Trends in Ecology and Evolution **33**:74-84.

Giery, S. T., and C. G. Layman. 2019. Ecological consequences of sexually selected traits: An eco-evolutionary perspective The Quarterly Review of Biology **94**:29-74.

Gowaty, P. A., and S. P. Hubbell. 2009. Reproductive decisions under ecological constraints: it's about time. Proceedings of the National Academy of Sciences **106**:10017-10024.

Hedrick, A. V., and E. J. Temeles. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. Trends in Ecology & Evolution **4**:136-138.

Janicke, T., M. G. Ritchie, E. H. Morrow, and L. Marie-Orleach. 2018. Sexual selection predicts species richness across the animal kingdom. Proceedings of the Royal Society of London Series B. **285**:20180173.

Jones, M. 1997. Character Displacement In Australian Dasyurid Carnivores: Size Relationships And Prey Size Patterns. Ecology **78**:2569-2587.

Kidwell, J. F., M. T. Clegg, F. M. Stewart, and T. Prout. 1977. Regions of stable equilibria for models of differential seleciton in the two sexes under random mating. Genetics:171-183.

Kitano, J., S. Mori, and C. L. Peichel. 2007. Sexual dimorphism in the external morphology of the threespine stickleback (Gasterosteus aculeatus). Copeia **2**:336-349.

Kitano, J., S. Mori, and C. L. Peichel. 2012. Reduction Of Sexual Dimorphism In Stream-Resident Forms Of Three-Spined Stickleback Gasterosteus Aculeatus. Journal of Fish Biology **80**:131-146.

Kohorn, L. 1994. Shoot Morphology And Reproduction In Jojoba - Advantages Of Sexual Dimorphism. Ecology **75**:2384-2394.

Kohorn, L. 1995. Geographic-Variation In The Occurrence And Extent Of Sexual Dimorphism In A Dioecious Shrub, Simmondsia-Chinensis. Oikos **74**:137-145.

Kokko, H., I. Booksmythe, and M. D. Jennions. 2013. Causality and sex roles: prejudice against patterns? A reply to Ah-King. Trends in Ecology and Evolution **28**:2-4.

Krause, M. A., and G. M. Burghardt. 2007. Sexual Dimorphism Of Body And Relative Head Sizes In Neonatal Common Garter Snakes. Journal of Zoology **272**:156-164.

Lehtonen, J., G. A. Parker, and L. Schärer. 2013. Why anisogamy drives ancestral sex roles. Evolution **70**:1129-1135.

Leinonen, T., J. M. Cano, and J. Merila. 2011. Genetic Basis Of Sexual Dimorphism In The Threespine Stickleback Gasterosteus Aculeatus. Heredity **106**:218-227.

Levenson, H. 1990. Sexual Size Dimorphism In Chipmunks. Journal of Mammalogy **71**:161-170.

Maend, R., E. Rasmann, and M. Maegi. 2013. When A Male Changes His Ways: Sex Differences In Feeding Behavior In The Pied Flycatcher. Behavioral Ecology **24**:853-858.

Maklakov, A., S. J. Simpson, F. Zajitchek, M. D. Hall, J. Dessmann, F. Clissold, D. Raubenheimer, R. Bondurianksy, and R. C. Brooks. 2008. Sex-specific effects of nutrient intake on reproduciton and lifespan Current Biology **18**:1062-1066.

Martin, J. L., and J. Pitocchelli. 1991. Relation Of Within-Population Phenotypic Variation With Sex, Season, And Geography In The Blue Tit. Auk **108**:833-841.

Nosil, P., and T. Reimchen. 2005. Ecological opportunity and levels of morphological variance within freshwater stickleback populations. Biological Journal of the Linnean Society **86**:297-308.

Oke, K. B., E. Motivans, T. P. Quinn, and A. P. Hendry. 2018. Sexual dimorphism modifies habitat-associated divergence: Evidence from beach and creek breeding sockeye salmon. Journal of Evolutionary Biology **32**:227-242.

Parker, G. A. 2014. The Sexual Cascade and the Rise of Pre-Ejaculatory (Darwinian) Sexual Selection, Sex Roles, and Sexual Conflict. Cold Spring Harbor Perspectives in Biology **6**:a017509.

Parker, G. A., and T. Pizzari. 2015. Sexual selection: the logical imperative.*in* T. Hoquet, editor. Current Perspectives on Sexual Selection. Springer, Dordrecht.

Parsons, K. J., J. Wang, G. Anderson, and R. C. Albertson. 2015. Nested Levels Of Adaptive Divergence: The Genetic Basis Of Craniofacial Divergence And Ecological Sexual Dimorphism. G3 **5**:1613-1624.

Pasinelli, G. 2000. Sexual Dimorphism And Foraging Niche Partitioning In The Middle Spotted Woodpecker Dendrocopos Medius. Ibis **142**:635-644.

Pearson, D., R. Shine, and R. How. 2002. Sex-Specific Niche Partitioning And Sexual Size Dimorphism In Australian Pythons (Morelia Spilota Imbricata). Biological Journal of the Linnean Society **77**:113-125.

Perry, J. C., C. J. Garroway, and L. Rowe. 2017. The role of ecology, neutral processes and antagonistic coevolution in an apparent sexual arms race. Ecology Letters **20**:1107-1117.

Pfennig, D. W., and K. S. Pfennig. 2012. Evolution's wedge: competition and the origins of diversity. University of California Press, Berkeley, CA.

Pincheira-Donoso, D., T. Tregenza, R. K. Butlin, and D. J. Hodgson. 2018. Sexes and species as rival units of niche saturation during community assembly. Global Ecology and Biogeography **27**:593-603.

Power, H. W. 1980. The foraging behavior of mountain bluebirds with emphasis on sexual foraging differences Ornithological Monographs **28**:1-72.

Price, T. D. 1984. The evolution of sexual size dimorphism in Darwin's finches. The American Naturalist **123**:500-518.

Queral-Regil, A., and R. B. King. 1998. Evidence For Phenotypic Plasticity In Snake Body Size And Relative Head Dimensions In Response To Amount And Size Of Prey. Copeia **2**:423-429.

Reddiex, A. J., T. P. Gosden, R. Bonduriansky, and S. F. Chenoweth. 2013. Sex-specific fitness consequences of nutrient intake and the evolvability of diet preferences. The American Naturalist **182**:91-102.

Reimchen, T., and P. Nosil. 2004. Variable Predation Regimes Predict The Evolution Of Sexual Dimorphism In A Population Of Threespine Stickleback. Evolution **58**:1274-1281.

Reimchen, T. E., and P. Nosil. 2001. Ecological causes of sex-biased parasitism in three-spined stickleback. Biological Journal of the Linnean Society **73**.

Rowe, L., S. F. Chenoweth, and A. F. Agrawal. 2018. The genomics of sexual conflict. The American Naturalist **192**:274-286.

Roy, D., O. Seehausen, and P. Nosil. 2013. Sexual dimorphism dominates divergent host plant use in stick insect morphoogy. BMC Evolutionary Biology **13**:135.

Rueffler, C., T. J. M. Van Dooren, O. Leimar, and P. A. Abrams. 2006. Disruptive selection and then what? Trends in Ecology & Evolution **21**:238-245.

Schluter, D. 2000a. Ecological character displacement and speciation in sticklebacks. The American Naturalist **140**:85-108.

Schluter, D. 2000b. The ecology of adaptive radiation. Oxford University Press, Oxford:.

Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. The Condor **68**:113-151.

Shärer, L., L. Rowe, and G. Arnqvist. 2012 Anisogamy, chance and the evolution of the sex roles. Trends in Ecology & Evolution **27**:260-264.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quarterly Review of Biology **64**:419-461.

Shine, R., R. N. Reed, S. Shetty, and H. G. Cogger. 2002. Relationships Between Sexual Dimorphism And Niche Partitioning Within A Clade Of Sea-Snakes (Laticaudinae). Oecologia **133**:45-53.

Simmons, L. W. 1987. Competition Between Larvae Of The Field Cricket, Gryllus-Bimaculatus (Orthoptera, Gryllidae) And Its Effects On Some Life-History Components Of Fitness. Journal of Animal Ecology **56**:1015-1027.

Slatkin, M. 1984. Ecological causes of sexual dimorphism. Evolution **38**:622-630.

Spoljaric, M. A., and T. Reimchen. 2008. Habitat-dependent reduction of sexual dimorphism in geometric body shape of haida gwaii threespine stickleback. Biological Journal of the Linnean Society **95**:505-516.

Stamps, J. A., J. B. Losos, and R. M. Andrews. 1997. A comparative study of population density and sexual size dimorphism in lizards. American Naturalist **149**:64-90.

Stuart, Y. E., and J. B. Losos. 2013. Ecological character displacement: glass half full or half empty? Trends in Ecology & Evolution **28**:402-408.

Summers, R. W., S. Smith, M. Nicoll, and N. K. Atkinson. 1990. Tidal And Sexual Differences In The Diet Of Purple Sandpipers Calidris-Maritima In Scotland. Bird Study **37**:187-194.

Svardal, H., C. Rueffler, and M. Doebeli. 2014. Organismal complexity and the potential for evolutionary diversification. Evolution **68**:3248-3259.

Svensson, E. I. 2019. Eco-evolutionary dynamics of sexual selection and sexual conflict Functional Ecology **33**:60-72.

Thom, M. D., L. A. Harrington, and D. W. Macdonald. 2004. Why Are American Mink Sexually Dimorphic? A Role For Niche Separation. Oikos **105**:525-535.

Tibbetts, E. A., and R. J. Safran. 2009. Co-Evolution Of Plumage Characteristics And Winter Sociality In New And Old World Sparrows. Journal of Evolutionary Biology **22**:2376-2386.

Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136-179 *in* B. Campbell, editor. Sexual selection and the descent of man. Aladine, Chicago.

Viranta, S., and K. Kauhala. 2011. Increased Carnivory In Finnish Red Fox Females - Adaptation To A New Competitor? Annales Zoologici Fennici **48**:17-28.

Wan, Y., R.-C. Quan, G.-P. Ren, L. Wang, Y.-C. Long, X.-H. Liu, and J.-G. Zhu. 2013. Niche Divergence Among Sex And Age Classes In Black-And-White Snub-Nosed Monkeys (Rhinopithecus Bieti). International Journal of Primatology **34**:946-956.

Yun, L., P. J. Chen, K. E. Kwok, C. S. Andell, H. D. Rundle, and A. F. Agrawal. 2018. Competition for mates and the improvement of nonsexual fitness.201804335.

Zajitschek, F., and T. Connallon. 2017. Partitioning of resources: the evolutionary genetics of sexual conlflict over resource acquisition and allocation. Journal of Evolutionary Biology **30**:826-838.

Supplementary Material

Details of Literature Review

To ascertain existing evidence for ECD between the sexes, I reviewed all published articles citing Slatkin's 1984 *Evolution* paper as reported by ISI Web of Science (n = 376 as of January 2019). This literature search of citations to Slatkin 1984 was performed because: 1) the goal was to identify a body of papers that would be likely to have tested the hypothesis of ECD between the sexes explicitly, if such studies exist, and 2) Slatkin 1984 represents the first theoretical formalization of ECD between the sexes (as well as other ecological models of dimorphism). Thus, carefully-designed empirical tests of the hypothesis of ECD would be very likely to have cited this paper. For each relevant paper I examined whether the study presented evidence in support of or refuting the criteria listed in Box1; note that I assessed relevance regardless of whether authors of the studies in question framed their results as tests of ECD. Papers were deemed relevant if empirical and examining evidence or consequences of sex differences in some trait of potential ecological importance. I did not consider papers focused solely on sex differences in traits clearly related only to mating success (with no evidence or suggestion by the authors of any ecological importance), or papers focused solely on the evolution of genetic constraints on sexual dimorphism (for which this paper is also frequently cited for). My assessment was generous, and for some criteria, particularly IV, evidence was often speculative or indirect, and such results are noted with asterisks in corresponding tables. An example of ‘indirect’ evidence of criteriun IV could, for example, include demonstration of correlations between the expression of sexual dimorphism and some ecological variable which is speculated (but not shown) to represent variation in the strength of resource competition, such as winter foraging habitat. This review yielded 212 empirical studies reporting some evidence either in support of or refuting at least one criterion for ECD (full list, including the 376 papers identified in the ISI search and assessment of the 212 papers deemed relevant, is provided as a Supplementary excel file). Excluding the majority of these studies that only report sex differences in a trait of potential ecological relevance (Criterion I) yielded 43 studies that indicate some additional support for the hypothesis of ECD between the sexes (including two studies with some evidence of convergent character displacement; Box 2 Table 1). This assessment of existing evidence for ECD between the sexes is conservative; although many studies likely exist that report some evidence for ECD that do not cite Slatkin 1984, this search could be seen as an assessment of studies that were perhaps most likely to provide a test of ECD given their reference lists.