



## SYMPOSIUM

### Cross-sexual Transfer Revisited

Andrew P. Anderson <sup>\*,†</sup> and Jay Jinsing Falk <sup>†‡</sup>

\*Biology Department, Reed College, Portland, OR 97202, USA; †Department of Biology, University of Washington, Seattle, WA 98195, USA; ‡Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, CO 80309, USA

From the symposium “Sexual diversity and variation” presented at the annual meeting of the Society for Integrative and Comparative Biology virtual annual meeting, January 16–March 31, 2023.

<sup>1</sup>E-mail: [aquaticdrew@gmail.com](mailto:aquaticdrew@gmail.com)

**Synopsis** In her influential book “Developmental Plasticity and Evolution,” Mary Jane West-Eberhard introduced the concept of cross-sexual transfer, where traits expressed in one sex in an ancestral species become expressed in the other sex. Despite its potential ubiquity, we find that cross-sexual transfer has been under-studied and under-cited in the literature, with only a few experimental papers that have invoked the concept. Here, we aim to reintroduce cross-sexual transfer as a powerful framework for explaining sex variation and highlight its relevance in current studies on the evolution of sexual heteromorphism (different means or modes in trait values between the sexes). We discuss several exemplary studies of cross-sexual transfer that have been published in the past two decades, further building on West-Eberhard’s extensive review. We emphasize two scenarios as potential avenues of study, within-sex polymorphic and sex-role reversed species, and discuss the evolutionary and adaptive implications. Lastly, we propose future questions to expand our understanding of cross-sexual transfer, from nonhormonal mechanisms to the identification of broad taxonomic patterns. As evolutionary biologists increasingly recognize the nonbinary and often continuous nature of sexual heteromorphism, the cross-sexual framework has important utility for generating novel insights and perspectives on the evolution of sexual phenotypes across diverse taxa.

#### Glossary

**Cross-sexual transfer**—process by which one sex acquires the trait values found in the other sex of a sexually heteromorphic ancestral species.

**Sex variation**—trait value distributions of a given phenotype for each sex.

**Sexual heteromorphism**—sex difference in the mean(s) and/or mode(s) of a trait value.

**Sexual mosaicism**—the concept that sexes are often heteromorphic for multiple phenotypes, but that within any given individual, each of these phenotypic traits can lie at different points of their respective population distributions.

**Sex-specific polymorphism**—discrete trait variation that is only found in one sex.

**Sex-role reversal**—a natural history where females are limited by access to male mates leading to stronger sexual selection in females.

#### Introduction

In 2003, Mary Jane West-Eberhard published her influential book “Developmental Plasticity and Evolution” (West-Eberhard 2003) that has since generated numerous discussions and thousands of citations in multiple fields across biology. A major theme of the book was the idea that associated traits can be reshuffled to generate novel trait combinations. In some cases, this can involve traits associated with sexual phenotypes. This was the subject of a book chapter, *Cross-sexual Transfer*. She defined **cross-sexual transfer** (See Glossary) as when “discrete traits that are expressed exclusively in one sex in an ancestral species appear in the opposite sex of descendants.” At its basis, cross-sexual transfer is a hypothesis about trait origins, offering a potential evolutionary and developmental process by which traits become expressed in one or both sexes. In the opening of the chapter, West-Eberhard observed that the development of both primary and secondary sexually heteromorphic traits (i.e., different means or modes in trait

values between the sexes) involve sex-specific regulatory mechanisms that often act differently on shared primordial structures. This developmental plasticity suggests that minor or no genomic changes may be necessary to achieve cross-sexual transfer, indicating that such a process could occur frequently. Cross-sexual transfer offers a description of how **sex variation** is generated within populations and is also a hypothesis for how phenotypic shifts can occur through small changes to regulatory processes over short evolutionary timescales. Given the prevalence of **sexual heteromorphisms** and variation across and within populations, species, and even larger taxonomic groups, cross-sexual transfer has likely occurred numerous times over evolutionary history.

As an illustration, one example West-Eberhard discussed in detail was the evolution of the pseudopenis in female spotted hyenas (*Crocuta crocuta*). Females of this species have enlarged phalluses that are nearly indistinguishable in the field from those of males (Kruuk 1973; Hamilton et al. 1986). Both sexes are capable of producing erections and use this as a frequent social display (Glickman et al. 2006). However, as with the vast majority of mammals, other hyena species are sexually heteromorphic with larger phalluses in males and smaller clitorises in females (Glickman et al. 2006). Thus, the monomorphy of spotted hyena phalluses must have been derived from a heteromorphic ancestor, pointing to the possibility that a cross-sexual transfer occurred from a former male-specific trait, to one that is now found in both sexes (West-Eberhard 2003). Did the female phallus evolve by cooping regulatory mechanisms from males, or did it evolve entirely independently? Developmental observations have shown that both female and male phalluses are derived from the same primordial structure (West-Eberhard 2003; Cunha et al. 2014), lending strong evidence to a hypothesis that at least some aspect of the regulatory mechanisms that produce larger phalluses has been transferred from sperm-producing individuals to all individuals of the species.

While this example pertains to a trait that is directly related to sexual reproduction, cross-sexual transfer can be applied to a variety of discrete and continuous traits, including color, size, physiology, and behavior. In fact, in addition to its utility as a hypothesis, cross-sexual transfer offers researchers an important framework for considering the evolution of variation between and within the sexes. There has been a recent and growing acknowledgment that sex itself is best understood as a nonbinary, multimodal, and multivariate type of diversity (Mank 2022; Richardson 2022; McLaughlin et al. 2023—This issue). We suggest that the cross-sexual transfer framework centers this perspective of sexual phenotypes while incorporating a critical pathway to understanding these traits as dynamic and evolvable.

Indeed, West-Eberhard repeatedly invoked a concept of **sex mosaicism** throughout her chapter. In one particular instance, her perspective lends itself even further to the nonbinary nature of sexes:

*Because the sexual phenotype of any species is a mosaic of sub-units, there are many kinds of “intersexes” that amount to continuous variation... One evolutionary consequence of this is that many degrees of change are possible, from partial sex transformation, involving a single small trait, to complete role reversals with extensive morphological change. —West-Eberhard (2003)*

By viewing sexes as groupings of correlated traits, it is only logical that every individual in a population is likely to be in some way a form of “intersex” because every individual likely contains traits that are more commonly found in the other sex. Cross-sexual transfer may be more overtly noticeable, or perhaps clearly adaptable in some species (Box 1). However, the cross-sexual transfer process may be a near-ubiquitous phenomena occurring to some degree in all individuals. We believe both of these possibilities should be considered end points of a spectrum of cross-sexual possibilities and cite examples of such throughout the proceeding sections.

#### **Box 1 The adaptivity of cross-sexual transfer**

In this manuscript, we discuss how traits that have undergone cross-sexual transfer may be adaptive and how cross-sexual transfer may affect a population's adaptive potential. Cross-sexual transfer, however, is a process that causes variation in trait values within and across sexes in a population. While selection can act on traits produced by cross-sexual transfer, the framework makes no claims about adaptation. As with all traits, care should be taken when invoking adaptive explanations for trait values produced by cross-sexual transfer without investigating relative fitness, correlated traits, and other evolutionary mechanisms (e.g., genetic drift).

As the concepts of sexual trait-value continua and sex diversity continue to be studied and become more included in research on sexual heteromorphism, we urge biologists to revisit cross-sexual transfer as a framework for understanding sex variation. Despite its clear utility for research within and among species, we argue that cross-sexual transfer is under-utilized in empirical studies today. As we show in this paper, fascinating examples of cross-sexual transfer are currently being published, but do not invoke cross-sexual transfer in their discussions. This inhibits a unified discourse and prevents us from discerning the wider impact of cross-sexual transfer. Further, framing evolutionary and comparative questions through a cross-sexual transfer lens would encourage researchers to consider the

multivariate and multimodal nature of sex (McLaughlin et al. 2023) from a dynamic evolving perspective. The goal of this review is to reintroduce the concept to the scientific community, provide current examples to highlight the concepts and utility of the cross-sexual transfer framework, and propose future directions.

Though we attempted to gather many examples published since West-Eberhard's publication in 2003, this should not be considered a completely exhaustive review. We are limited by space to provide the extensive detail of the *Cross-Sexual Transfer* chapter and we strongly recommend readers refer to the original source after reading here.

### Historic and current use of cross-sexual transfer

Given the potential ubiquity of cross-sexual transfers, we began by investigating the number of mentions of the terms “cross-sexual transfer” and “cross sexual transfer” using two search databases: Google Scholar and SCOPUS. We did not limit the years or types of publications in our search in an effort to capture the full use of the term, but no mention of the term appeared prior to West-Eberhard's publication in either database. In all, Google Scholar reported 27 publications and SCOPUS just 5 with complete overlap in findings (Supplementary Table S1). While there are some excellent perspectives and reviews that engage in the concept of cross-sexual transfer (Ketterson 2007; Bonduriansky 2011; Westrick et al. 2022; Anderson and Renn 2023), we found just eight experimental papers that invoke the concept anywhere in the paper and only six that offer it as an explanation for the observed pattern. Only one paper specifically sought to test evidence of cross-sexual transfer (Staub 2021), while another provides and acknowledges the evidence it found is in line with cross-sexual transfer (Reinhardt et al. 2007). As we have discussed, there are several reasons why this type of evolutionary shift should be relatively common, making the limited discourse on the topic an indication that cross-sexual transfer as a concept needs to be more widely considered in the scientific community. Despite our finding that mentions of cross-sexual transfer is uncommon, we found numerous examples of studies that provide evidence for this exact process but do not invoke the term. While the term itself is not necessary for good research, using and mentioning the cross-sexual framework provides a common ground for discussing a phenomenon that integrates a plethora of biological fields, including development, evolution, genetics, endocrinology, physiology, and more. To encourage more empirical and theoretical application, we next detail what types of observations lend support to the cross-sexual transfer hypothesis.

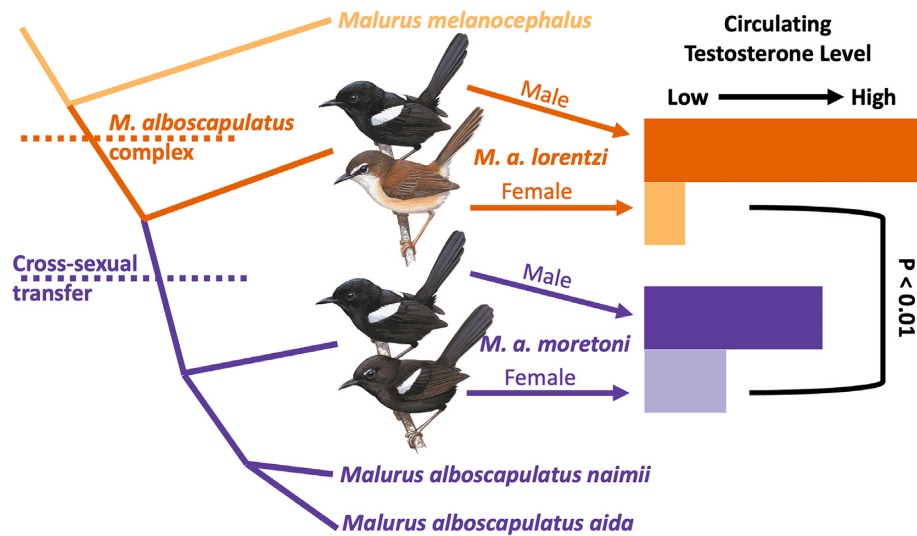
### Understanding the evidence

Multiple types of evidence support the possibility of cross-sexual transfer (Box 2). The evolutionary process of cross-sexual transfer begins with sexual heteromorphism (i.e., distinct means or modes in trait values between the sexes) and ends with one sex secondarily acquiring one or more trait values of the other sex. The sex that originally bore the trait value may maintain its original trait values (secondary monomorphism) or evolve its own new trait value distribution (heteromorphic shift). This process may occur over individual or generational timescales and does not presume specific mechanisms or selective pressures mediating the transfer. Sexes can diverge either by increasing the distance between modes of variation in traits, or by evolving a myriad of new specializations unique to one sex. Even when sexes are highly heteromorphic, the transfer of traits across sexes may be activated through regulatory mechanisms rather than the evolution of traits de novo (Ketterson 2007; Westrick et al. 2022; Anderson and Renn 2023).

#### Box 2 Evidence for cross-sexual transfer: Suggested indicators of putative cross-sexual transfer taken from West-Eberhard (2003)

- (1) Trait comprised of characteristics more typical of the other sex in the same or related species.
- (2) Trait present in a subset of one sex that resembles the other sex in a heteromorphic species.
- (3) Trait present in both sexes but phylogenetic information suggests heteromorphic ancestor (secondary monomorphism).
- (4) Trait value in the secondary sex is not fully equal to the ancestrally bearing sex, but is closer to the trait value of the ancestrally bearing sex than other members of the secondary sex within the population or across species.
- (5) Trait has maladaptive features in one sex, the secondary sex, due to interference with typical functions of that sex, but not the other, ancestral sex.
- (6) Hormone manipulations (involving hormones with high circulating levels in the ancestral sex) indicate trait can be induced in the other, secondary sex.
- (7) Lack of evidence of alternative explanations:
  - (a) primary monomorphism;
  - (b) convergence;
  - (c) deletion and regression of heteromorphic traits;
  - (d) sex-expression pathologies via parasites.

Since cross-sexual transfer uses sexual heteromorphism as its starting point, we will not discuss the



**Fig. 1** White-Shouldered Fairywren, *M. alboscapulatus*, as an example of cross-sexual transfer. Phylogeny of the four *M. alboscapulatus* subpopulations and the sister species *M. melanocephalus* (female has brown shoulder). All subpopulations except for *M. a. lorentzi*, the ancestral lineage, have females with white shoulders. Circulating testosterone levels in wild female *M. a. moretoni* (white shoulder) are higher than in wild female *M. a. lorentzi* (brown shoulder). Testosterone implants induce white shoulder phenotype in *M. a. lorentzi* females. Data for the figure were taken from [Enbody et al. \(2018\)](#) and [Enbody et al. \(2022\)](#). Illustrations by Hilary Burn © Lynx Edicions.

evolutionary origin of sex-biased regulation here (but see [Anderson and Renn 2023](#)). However, because the hypothesis pertains to traits “originating” in one sex, cross-sexual transfer cannot be discussed without phylogenetic context. Indeed, phylogenetic or population patterns of sexual heteromorphism offer three types of evidence in support of cross-sexual transfer ([Box 2](#)). The fourth and fifth types of evidence are perhaps less reliable because they assume there may be a slight difference in either trait expression or adaptivity in the ancestral versus derived trait-bearing sex, neither of which are necessarily true (see also [Box 2](#)). The sixth kind of evidence focuses on the signal that triggers sex-biased expression, in this case, hormonal regulation. This concept of sex-biased signal and cooption by the other sex has received further attention in other reviews ([Ketterson 2007](#); [Westrick et al. 2022](#); [Anderson and Renn 2023](#)), but here we interpret this to mean some regulatory pattern (hormonal or otherwise) can be accessed by the secondary sex to produce the same trait.

As a case study, we implement this framework in the White-Shouldered Fairywren (*Malurus alboscapulatus*, [Fig. 1](#)), where multiple types of evidence for cross-sexual transfer can be found. Across all populations, males have a white epaulet on their shoulders, but females only have this ornamental trait in certain populations ([Box 2](#), evidence type 1). Further, while the white epaulet is substantial on females that bear it, coloration is not as complete as found in males ([Box 2](#), evidence type 4). The white epaulet can be induced with testosterone in females that naturally lack the trait

and females that bear the trait have higher circulating testosterone than those females that do not ([Enbody et al. 2018](#); [Box 2](#), evidence type 6). Lastly, and crucially, the ancestral population was determined to be those without trait-bearing females ([Box 2](#), evidence type 3) and females in the sister species, Red-Backed Fairywren, also lack these white epaulets ([Enbody et al. 2022](#)), thereby resolving the evolutionary history of the trait. Taken together, the evidence points to a cross-sexual transfer with the gain of the epaulet by females via developmental regulation from testosterone that was initially male biased.

Another interesting phenomenon to investigate using the cross-sexual transfer framework is male nipples and lactation in mammals. In mammals, nipples are part of the lactation/nursing phenotype and are typically expressed in both sexes but are only functional in females ([Box 2](#), evidence types 2 and 3). [Gould \(1993\)](#) suggested nipples bear little fitness cost to males and the developmental programming to generate them is shared between the sexes. Nipples are likely an ancestral or primary monomorphism, evidenced by the majority of male mammals in possession of nipples; thus nipples are not gained in males via cross-sexual transfer, but rather they have not been fully lost. However, without definitive knowledge of the ancestral state, a cross-sexual transfer early on in the mammalian lineage cannot be ruled out (see also [West-Eberhard’s description of naked-mole rats, 2003](#)). While a part of the lactation/nursing phenotype, the presence of nipples can be considered separately from the actual physiological

response of lactation. Exogenous hormones from hormone replacement therapies, phytoestrogens, or pollutants can induce lactation (Kunz and Hosken 2009) suggesting there is potential for cross-sexual transfer of lactation. This potential has been realized in natural populations of two species of bat where healthy males have been found lactating with no signs of any developmental, nutritional, or environmental deficiencies (Kunz and Hosken 2009). While this is clearly a cross-sexual transfer from female to male, there is no evidence of males nursing pups and therefore no clear adaptive function (Box 1). Nevertheless, this finding is a striking example of cross-sexual transfer of a particular phenotype, lactation, that is considered sex-specific across mammals.

### Distinguishing alternatives

While evidence in support of cross-sexual transfer abounds across traits and systems, at least two alternative explanations should be considered: convergence and regression (Fig. 2). Convergence is the independent evolution of similar phenotypes across the sexes that arise from differences in genotype/gene expression. Given the sexes share a genome, convergence is a less parsimonious hypothesis than cross-sexual transfer, since the latter only requires the adoption of a developmental pattern already present in the other sex. Analogous features evolved from convergence could be detected by the expression of different gene sets during activity or development. This has been found in duetting Forest Weavers, which have different transcriptional patterns and active brain regions during the duet (Gahr et al. 2008). In another example, monogamous male and female deer mice seem to express different genes when engaging in parental care (Bendesky et al. 2017). We note that some gene expression overlap is likely to occur even in the production of analogous traits, making it hard to disentangle convergence and cross-sexual transfer purely through transcriptomics. However, even if this type of gene expression overlap does occur under convergent evolution, the developmental signaling pathway that triggers a trait (e.g., hormones) should still be distinct in the case of convergence and shared in the case of cross-sexual transfer (Anderson and Renn 2023). Distinguishing and observing developmental triggers is therefore one potential avenue for more robust testing for convergent evolution.

Regression to a monomorphic ancestral state is another alternative to cross-sexual transfer, and is likely more common than convergence. In long-fingered frogs, the third digit of males can reach up to 40% of the total body length. A phylogenetic reconstruc-

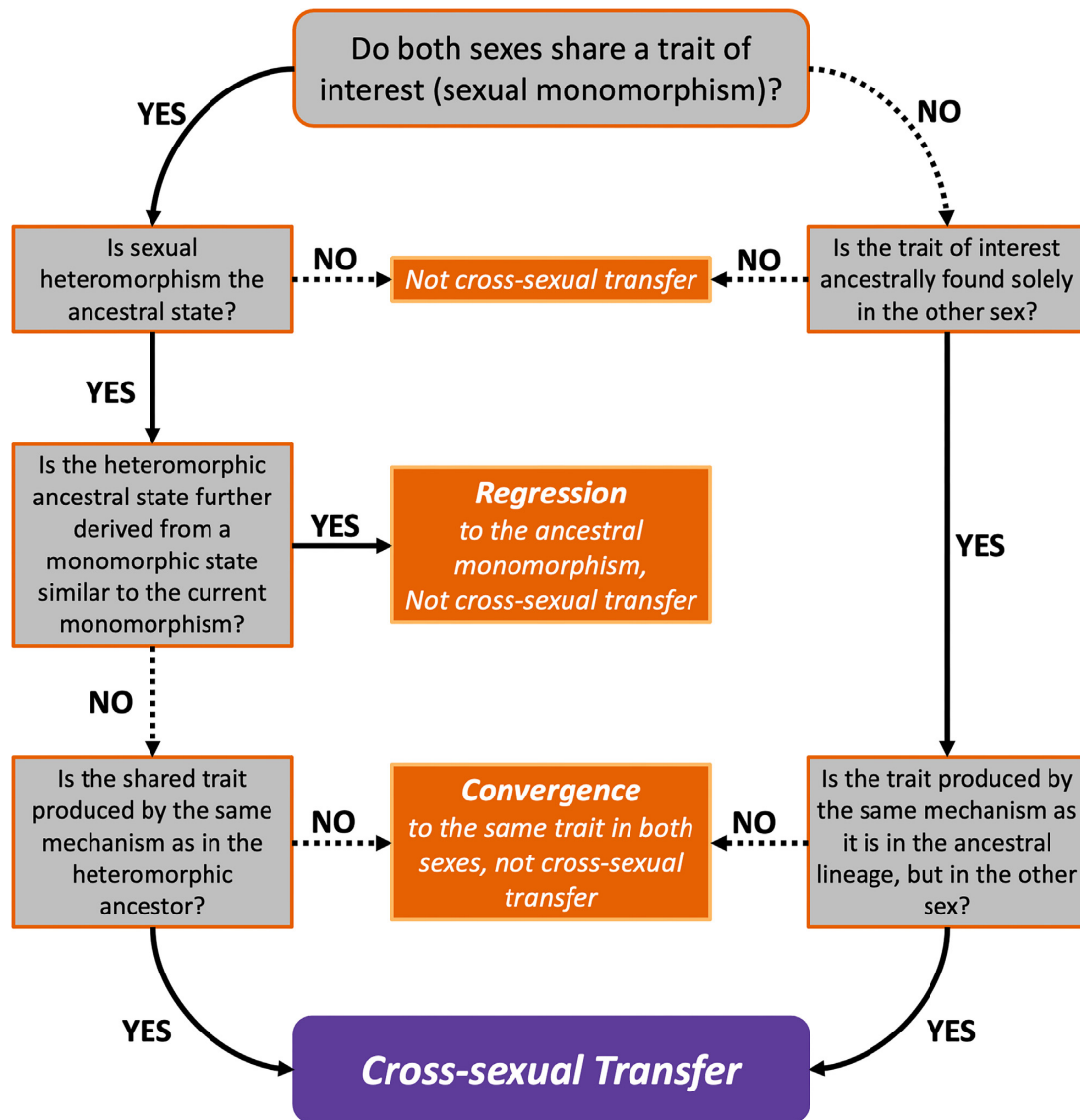
tion demonstrates this long digit heteromorphism was gained from a monomorphic state with small digits (Blackburn 2009). Some species in this group evolved from this heteromorphic state toward a monomorphic one where males have reduced their digit length to that of females (Blackburn 2009). This would not be considered cross-sexual transfer as this is a return to the ancestral, monomorphic state. Conversely, narrow heads and shorter bodies in both sexes was the ancestral state in a group of salamanders (Staub 2021). Heteromorphism emerged with increased head width and longer bodies in males and in more derived species, the females “caught up” to these male sizes (Staub 2021). This would be considered cross-sexual transfer as the monomorphisms of the derived species are of different trait values than the ancestral monomorphism, but went through a heteromorphic transition.

### Where to look for cross-sexual transfer

#### Polymorphisms

**Sex-specific polymorphisms** (i.e., sex-limited polymorphisms), where one sex is polymorphic but not the other, are common and provide a uniquely rich area to study the evolution of cross-sexual transfer. In many instances, one of the morphs in the variable sex can have similar trait values to the monomorphic sex, often rendering it difficult to distinguish one sex from the other. Because of their discrete nature in both form and development, polymorphisms can be clearly described and measured, aiding in understanding of how different traits have evolved over time. The similarity of trait values between one morph of the polymorphic sex and the monotypic sex could be a result of cross-sexual transfer but convergence must be tested as well (Fig. 2). Additionally, within-sex polymorphism can show “mixing” of male and female traits (Mank 2022), which provides insights into how different sexes have evolved in relation to one another, which traits are more likely to undergo cross-sexual transfer, and how often cross-sexual transfers occur in these systems.

Some examples of the applicability of cross-sexual transfer in describing sexual polymorphism include some hummingbird species such as the white-necked jacobin (Falk et al. 2021, 2022). Females are polymorphic, with roughly 20% having plumage that is similar to males. Males are on average more aggressive than females, and females that mimic them experience fewer attacks from other hummingbirds simply by appearing like them, without engaging in dangerous and energetically costly agonistic behaviors (Falk et al. 2022). Similar female polymorphisms have evolved repeatedly in hummingbirds, and phylogenetic



**Fig. 2** A flowchart for distinguishing cross-sexual transfer from alternative hypotheses. Questions are shaded gray, and conclusions in purple/orange. Both sexes may currently express a trait that was ancestrally only found in one sex (left side of chart). If the trait is currently heteromorphic (right side of chart), one sex currently expresses a trait that was ancestrally only found in the other sex, but the sex that first expressed the trait has subsequently changed or lost the trait. This particular type of cross-sexual transfer could pass through an intermediate monomorphic stage, though evidence of such may or may not persist in phylogenies of extant species.

analyses show that the likely ancestral state of female polymorphism is complete sexual heteromorphism rather than monomorphism (Diamant et al. 2021). Male-like plumage in females therefore likely developed through a cross-sexual transfer from traits that first evolved in males, but further research on the genetic and developmental basis of the trait is necessary to make a stronger conclusion. Though sex-specific polymorphisms are widespread across taxa and have recently attracted increasing attention (Mank 2022), only a few studies have been explicitly considered through the cross-sexual framework (Colonello-Frattini et al.

2010; Beani et al. 2014; Hartfelder et al. 2018; Willink et al. 2019).

Another fascinating example of putative cross-sexual transfer in sex-specific polymorphisms comes from a species of bat bug, *Afrocimex constrictus*, where two cross-sexual transfers have occurred, one resulting in a female polymorphism (Reinhardt et al. 2007). Like the related bed bugs, *A. constrictus* has hypodermic insemination and females have evolved a structure to reduce the costs of insemination. Males are often indiscriminate in their mating, leading to intrasexual inseminations. In response, *A. constrictus* males have evolved

structures similar to those found in females to reduce bodily harm, yet with slight differences that may cue the inseminating individual that their target is male. These structures, called paragenital sinuses, are small openings on the abdomen that are more “open” in males where the intromittent organ would be inserted. This possible cross-sexual transfer is interesting on its own, but the evolutionary story continues with yet another potential cross-sexual transfer. The structures that cue inseminating individuals that they have encountered a male are present in a portion of the female population, making females polymorphic. These females are inseminated roughly the same as males and less often than their “typical” female counterparts, which have more “closed” paragenital sinuses. Bat bugs are therefore notable for demonstrating a selective advantage to cross-sexual transfer by reducing harm of insemination in males, and reducing encounters for females. Increased fitness for females through reduced sexual conflict has also been demonstrated in damselflies with female-specific polymorphism (Takahashi et al. 2014).

### Sex-role reversals

Other systems where cross-sexual transfers might be readily observed are **sex-role reversed** species. While the term sex-role reversed has numerous and misleading meanings (Ah-King and Ahnesjö 2013), we use it to imply that selection pressures have created a situation where females are the mate-limited sex (Fritzsche et al. 2021). In these species, females may be mate-limited through part (e.g., bushcrickets—Ritchie et al. 1998; two-spotted goby—Forsgren et al. 2004) or all of their lifetime (e.g., jacanas—Jenni and Betts 1978; Gulf pipefish—Jones et al. 2001), which leads to greater sexual selection in females. As a result of female-biased sexual selection, cross-sexual transfer could putatively cause traits associated with sexual selection (e.g., ornamentation and mate choice) to appear in different sexes.

The challenge for researchers studying cross-sexual transfer in sex-role reversed species is the lack of a shared trait value across some members of both sexes as is found in sex-specific polymorphisms. As a result, there are two possibilities when observing a heteromorphic trait such as ornamentation: (1) the trait is not a product of cross-sexual transfer and has only ever been expressed in one sex throughout the evolutionary history of that trait or (2) the trait is a product of cross-sexual transfer and the original bearing sex no longer expresses that trait value. The best test of cross-sexual transfer is having a solid phylogenetic history of the trait. For example, in Gulf pipefish, *Syngnathus scovelli*, females are the mate-limited sex and have iridescent bands, which may play a role in male mate-choice

(Flanagan et al. 2014; Anderson and Jones 2019), a pattern missing from both males and females of closely related congeners (Stiller et al. 2022). This information indicates that iridescent bands evolved de novo in females and are not a product of cross-sexual transfer. Conversely, female smooth guardian frogs, *Limnonectes palavanensis*, call more frequently than males during courtship and have been observed in female-biased leks suggesting females are mate-limited (Goyes Vallejos et al. 2017). Calling and advertisement is male-biased throughout anurans suggesting this high occurrence of female calling may be a form of cross-sexual transfer.

Anderson and Renn (2023) propose that the mechanisms that control expression of a trait may indicate whether or not that trait is a product of cross-sexual transfer. Investigating the mechanistic controls of traits in sex-role reversed species, and other putative cases of cross-sexual transfer, may be especially informative (Eens and Pinxten 2000; Lipshutz and Rosvall 2020). The iridescent bands of female Gulf pipefish mentioned above are controlled by estrogen signaling (Partridge et al. 2010; Anderson et al. 2020), suggesting iridescent bands were initially developed in females and not through cross-sexual transfer from males. By contrast, the dark breast in female Barred Buttonquails (Muck and Goymann 2011), female nuptial coloration in female Red-Necked Phalaropes (Johns 1964), and female aggression in Black Coucals (Voigt and Goymann 2007) are all seemingly regulated through androgen pathways, which could point toward those female trait-values occurring as a result of cross-sexual transfer. Many of these examples lack strong phylogenetic evidence to verify a cross-sexual transfer by confirming that androgen signaling for these trait values emerged in a male ancestor. Therefore, while these examples are intriguing, confirming a heteromorphic ancestor would provide more concrete evidence. Anderson and Renn (2023) point out that circulating hormones may not be a precise indicator of which sex-biased hormone, if any, regulates a trait as there are multiple steps from hormone to biosynthetic conversion to receptor that occur within the cell. For example, some female-biased traits in sex-role reversed species may correlate with circulating progesterone (Lipshutz and Rosvall 2020); but at the cellular level, progesterone can be converted to androgens, thus females could be using the androgen signaling system at the cellular level but not the global level.

### Behavioral plasticity

The intersection between behavior, neural development, and evolution should be an especially fruitful

arena for the types of integrative investigations necessary to enrich the study of cross-sexual transfer. One behavior that is particularly well suited for this type of work is parental care, which we have not focused on because it has been recently and thoroughly reviewed (Dulac et al. 2014; Kohl and Dulac 2018; Westrick et al. 2022). Parental care is widespread and has evolved repeatedly in both sexes throughout the animal kingdom (Dulac et al. 2014). In some taxa, such as poison frogs (Dendrobatidae), parental care appears to be especially labile, with the evolution of male, female, and biparental care in a single clade as well as behavioral plasticity within species (West-Eberhard 2003; Westrick et al. 2022). As Westrick et al. (2022) emphasize, this diversity has and will continue to bridge the gap between the mechanisms that facilitate behavioral plasticity within sexes and the cross-species diversity in parental care mode. The study of parental care exemplifies how a cross-sexual transfer lens may facilitate integration across disparate fields, yielding new insights into how underlying mechanisms mediate major evolutionary transitions in life history.

### Implications of cross-sexual transfer

As we have previously discussed, the cross-sexual transfer framework employs a dynamic view of multimodal and multivariate sexes, offering a unique perspective on the evolution of sexual phenotypes. To illustrate just one example, Bonduriansky (2011) observed that sexual selection and sexual conflict, both forces that can cause sexual heteromorphism, allow species to “explore” the areas around adaptive peaks defined by viability selection. Subsequently, viability selection could then cause adaptive co-option of sex-biased traits through cross-sexual transfer when environments shift or new adaptive peaks are discovered (Bonduriansky 2011). We argue further that sexual heteromorphism can evolve for a number of reasons beyond sexual selection and conflict, and that any of these specializations could be adopted by the other sex if they become adaptive following an ecological change. It is therefore plausible to consider sexual heteromorphism as a sort of “reservoir” of standing variation or a readily available toolkit within a species that can be pulled into use under the right conditions. For example, in poison frogs, the evolution of biparental care from uniparental male care is associated with transitions to the use of smaller breeding pools (Brown et al. 2010). Therefore, ecological shifts or range expansions toward areas with less water may favor the evolution of cross-sexual transfer from ancestral male-only care to biparental care. In this case, female care is only advantageous in some environments, but the presence of care in males acts as a “reservoir”

of parental behavior that allows the species to more readily adapt to shifting environments through cross-sexual transfer to biparental care. The concept of sexes as reservoirs of adaptive change is similar to the hypothesis that species hybridization and genetic introgression can reduce species vulnerability in the face of rapid environmental change (Becker et al. 2013; Brauer et al. 2023). Cross-sexual transfer offers an analogous process between sexes rather than species. Unlike different species, sexes are part of the same genetic pool, facilitating rapid adaptive shifts through small evolutionary changes to a regulatory mechanism, or even plastic shifts within individuals based on environmental cues.

### Future directions and conclusion

West-Eberhard’s chapter on cross-sexual transfer proposed a general evolutionary pattern of trait recombination across the sexes and described ultimate and proximate patterns that might accompany shifts in trait value. In the two decades since its publication, hormone assays require smaller amounts of tissue, and the genomics revolution has transformed our ability to produce fine-scale phylogenies and test for homology through transcriptomics in nonmodel organisms. The potential to test and expand on the concept of cross-sexual transfer is therefore greater than ever. As some of the examples above have shown, much of this work is already being done, but is not specifically discussed in a cross-sexual framework. In the future, doing so will allow for improved comparisons and discussion of the phenomena across taxa.

Many outstanding questions could benefit from broader discussion and research. The Ancestral Modulation Hypothesis (Anderson and Renn 2023) is a framework that builds on cross-sexual transfer and is focused on identifying the specific genomic, transcriptomic, and hormonal patterns that underlie traits. In particular, the Ancestral Modulation Hypothesis predicts that the underlying genomic architecture responsible for the initial sexual heteromorphism is preserved during cross-sexual transfer, but the hormonal signaling cascade (hormone levels, receptor expression, and biosynthetic enzyme expression) has been altered in the secondarily bearing sex (genetically or environmentally) to access this architecture. In addition, there are outstanding genomic questions that seek to identify common changes that result in cross-sexual transfers. For example, are cross-sexual transfers more often the result of certain types of mutations? Inversion mutations are frequently implicated in rapid recombinatorial shifts (Faria et al. 2019), but other types of mutations (e.g., repeat expansions, duplications, or single-



gene changes) could result in changes to hormone or hormone-receptor expression levels. At a broad taxonomic level, have cross-sexual transfers occurred more often in some groups more than others? If so, why those specific taxa? Lastly, given the plasticity and diversity of cross-sexual transfers, what environmental pressures are more likely to induce shifts in sex-biased trait values both within an individual lifetime and over longer evolutionary spans?

We hope our description of cross-sexual transfer, how and where it can be investigated, and some striking examples of cross-sexual transfer has generated an interest in revisiting West-Eberhard's hypothesis. While we primarily focused on polymorphisms and sex-role reversals in this review, by no means do we imply these are the only, or even predominant groups where cross-sexual transfer occurs. In fact, West-Eberhard reviewed various taxonomic groups from plants to invertebrates to vertebrates and described numerous sex-biased and monomorphic species in which cross-sexual transfer likely occurred. Given the numerous examples of cross-sexual transfer initially described and contemporary examples provided here and in other reviews, we strongly encourage biologists to consider the possibility of cross-sexual transfer in their study systems. Many fascinating research programs that test these very concepts are underway, yet do not invoke cross-sexual transfer. Doing so will allow for a theoretical basis to compare and contrast the framework across taxa, and offers a springboard for exciting future developments.

## Funding Sources

AP Anderson is supported by the National Science Foundation Postdoctoral Research Fellowship in Biology Grant #2010841. JJ Falk is supported by the National Science Foundation Postdoctoral Research Fellowship in Biology Grant #2209192.

## Supplementary data

Supplementary data available at [ICB](https://icb.org) online.

## Conflict of Interest

The authors declare they have no conflicts of interest.

## Data Availability

Data from the literature search are available as Supplementary Data. No other novel data were used to generate this manuscript.

## References

- Ah-King M, Ahnesjö I. 2013. The “sex role” concept: an overview and evaluation. *Evol Biol* 40:461–70.
- Anderson AP, Flanagan SP, Rose E, Jones AG. 2020. The estrogen-responsive transcriptome of female secondary sexual traits in the Gulf pipefish. *J Hered* 111:294–306.
- Anderson AP, Jones AG. 2019. Choosy Gulf pipefish males ignore age but prefer active females with deeply keeled bodies. *Anim Behav* 155:37–44.
- Anderson AP, Renn SC. 2023. The Ancestral Modulation Hypothesis: predicting mechanistic control of sexually heteromorphic traits using evolutionary history. *Am Nat* (<https://doi.org/10.1086/725438>).
- Beani L, Dessi-Fulgheri F, Cappa F, Toth A. 2014. The trap of sex in social insects: from the female to the male perspective. *Neurosci Biobehav Rev* 46:519–33.
- Becker M, Gruenheit N, Steel M, Voelckel C, Deusch O, Heenan PB, McLenachan PA, Kardailsky O, Leigh JW, Lockhart PJ. 2013. Hybridization may facilitate in situ survival of endemic species through periods of climate change. *Nat Clim Change* 3:1039–43.
- Bendesky A, Kwon Y-M, Lassance J-M, Lewarch CL, Yao S, Peterson BK, He MX, Dulac C, Hoekstra HE. 2017. The genetic basis of parental care evolution in monogamous mice. *Nature* 544:434–9.
- Blackburn DC. 2009. Diversity and evolution of male secondary sexual characters in African squeakers and long-fingered frogs. *Biol J Linn Soc* 96:553–73.
- Bonduriansky R. 2011. Sexual selection and conflict as engines of ecological diversification. *Am Nat* 178:729–45.
- Brauer CJ, Sandoval-Castillo J, Gates K, Hammer MP, Unmack PJ, Bernatchez L, Beheregaray LB. 2023. Natural hybridization reduces vulnerability to climate change. *Nat Clim Change* 13:282–9.
- Brown JL, Morales V, Summers K. 2010. A key ecological trait drove the evolution of biparental care and monogamy in an amphibian. *Am Nat* 175:436–46.
- Colonello-Frattini NA, Guidugli-Lazzarini KR, Simões ZLP, Hartfelder K. 2010. Mars is close to venus—female reproductive proteins are expressed in the fat body and reproductive tract of honey bee (*Apis mellifera* L.) drones. *J Insect Physiol* 56:1638–44.
- Cunha GR, Risbridger G, Wang H, Place NJ, Grumbach M, Cunha TJ, Weldele M, Conley AJ, Barcellos D, Agarwal S, et al. 2014. Development of the external genitalia: perspectives from the spotted hyena (*Crocuta crocuta*). *Differentiation* 87:4–22.
- Diamant ES, Falk JJ, Rubenstein DR. 2021. Male-like female morphs in hummingbirds: the evolution of a widespread sex-limited plumage polymorphism. *Proc R Soc B* 288:20203004.
- Dulac C, O'Connell LA, Wu Z. 2014. Neural control of maternal and paternal behaviors. *Science* 345:765–70.
- Eens M, Pinxten R. 2000. Sex-role reversal in vertebrates: behavioural and endocrinological accounts. *Behav Processes* 51:135–47.
- Enbody ED, Boersma J, Schwabl H, Karubian J. 2018. Female ornamentation is associated with elevated aggression and testosterone in a tropical songbird. *Behav Ecol* 29:1056–66.
- Enbody ED, Sin SYW, Boersma J, Edwards SV, Ketaloya S, Schwabl H, Webster MS, Karubian J. 2022. The evolutionary history

- and mechanistic basis of female ornamentation in a tropical songbird. *Evolution* 76:1720–36.
- Falk JJ, Rubenstein DR, Rico-Guevara A, Webster MS. 2022. Intersexual social dominance mimicry drives female hummingbird polymorphism. *Proc R Soc B* 289:20220332.
- Falk JJ, Webster MS, Rubenstein DR. 2021. Male-like ornamentation in female hummingbirds results from social harassment rather than sexual selection. *Curr Biol* 31:4381–4387.e6.
- Faria R, Johannesson K, Butlin RK, Westram AM. 2019. Evolving inversions. *Trends Ecol Evol* 34:239–48.
- Flanagan SP, Johnson JB, Rose E, Jones AG. 2014. Sexual selection on female ornaments in the sex-role-reversed Gulf pipefish (*Syngnathus scovelli*). *J Evol Biol* 27:2457–67.
- Forsgren E, Amundsen T, Borg ÅA, Bjelvenmark J. 2004. Unusually dynamic sex roles in a fish. *Nature* 429:551–4.
- Fritzsche K, Henshaw JM, Johnson BD, Jones AG. 2021. The 150th anniversary of *The Descent of Man*: Darwin and the impact of sex-role reversal on sexual selection research. *Biol J Linn Soc* 134:525–40.
- Gahr M, Metzdorf R, Schmid D, Wickler W. 2008. Bi-directional sexual dimorphisms of the song control nucleus HVC in a songbird with unison song. *PLoS One* 3:e3073.
- Glickman SE, Cunha GR, Drea CM, Conley AJ, Place NJ. 2006. Mammalian sexual differentiation: lessons from the spotted hyena. *Trends Endocrinol Metab* 17:349–56.
- Gould SJ. 1993. Male nipples and clitoral ripples. *Columbia J Lit Art* 20:80–96.
- Goyes Vallejos J, Ulmar Grafe T, Ahmad Sah HH, Wells KD. 2017. Calling behavior of males and females of a Bornean frog with male parental care and possible sex-role reversal. *Behav Ecol Sociobiol* 71:1–12.
- Hamilton W, Tilson RL, Frank LG. 1986. Sexual monomorphism in spotted hyenas *Crocuta crocuta*. *Ethology* 71:63–73.
- Hartfelder K, Tiberio GJ, Lago DC, Dallacqua RP, Bitondi MMG. 2018. The ovary and its genes—developmental processes underlying the establishment and function of a highly divergent reproductive system in the female castes of the honey bee, *Apis mellifera*. *Apidologie* 49:49–70.
- Jenni DA, Betts BJ. 1978. Sex differences in nest construction, incubation, and parental behaviour in the polyandrous American jacana (*Jacana spinosa*). *Anim Behav* 26:207–18.
- Johns JE. 1964. Testosterone-induced nuptial feathers in phalaropes. *Condor* 66:449–55.
- Jones AG, Walker D, Avise JC. 2001. Genetic evidence for extreme polyandry and extraordinary sex-role reversal in a pipefish. *Proc R Soc Lond B* 268:2531–5.
- Ketterson ED. 2007. Perspective: masculinized dominant females in a cooperatively breeding species, a case of cross-sexual transfer? *Mol Ecol* 16:1345–7.
- Kohl J, Dulac C. 2018. Neural control of parental behaviors. *Curr Opin Neurobiol* 49:116–22.
- Kruuk H. 1973. Review of the spotted hyena. A study of predation and social behavior. *J Anim Ecol* 42:822–4.
- Kunz TH, Hosken DJ. 2009. Male lactation: why, why not and is it care? *Trends Ecol Evol* 24:80–5.
- Lipshutz SE, Rosvall KA. 2020. Neuroendocrinology of sex-role reversal. *Integr Comp Biol* 60:692–702.
- McLaughlin JF, Brock KM, Gates I, Pethkar A, Piattoni M, Rossi A, Lipshutz SE. 2023. Multimodal models of animal sex: breaking binaries leads to a better understanding of ecology and evolution. (<https://doi.org/10.1101/2023.01.26.525769>).
- Mank JE. 2023. Sex-specific morphs: the genetics and evolution of intra-sexual variation. *Nat Rev Genet* 24:44–52.
- Muck C, Goymann W. 2011. Throat patch size and darkness covaries with testosterone in females of a sex-role reversed species. *Behav Ecol* 22:1312–9.
- Partridge C, Boettcher A, Jones AG. 2010. Short-term exposure to a synthetic estrogen disrupts mating dynamics in a pipefish. *Horm Behav* 58:800–7.
- Reinhardt K, Harney E, Naylor R, Gorb S, Siva-Jothy MT. 2007. Female-limited polymorphism in the copulatory organ of a traumatically inseminating insect. *Am Nat* 170:931–5.
- Richardson SS. 2022. Sex contextualism. *Philos Theory Pract Biol* 14:2.
- Ritchie MG, Sunter D, Hockham LR. 1998. Behavioral components of sex role reversal in the tettigoniid bushcricket *Ephippiger ephippiger*. *J Insect Behav* 11:481–91.
- Staub NL. 2021. The evolution of derived monomorphism from sexual dimorphism: a case study on salamanders. *Integr Org Biol* 3:obaa044.
- Stiller J, Short G, Hamilton H, Saarman N, Longo S, Wainwright P, Rouse GW, Simison WB. 2022. Phylogenomic analysis of Syngnathidae reveals novel relationships, origins of endemic diversity and variable diversification rates. *BMC Biol* 20:1–21.
- Takahashi Y, Kagawa K, Svensson EI, Kawata M. 2014. Evolution of increased phenotypic diversity enhances population performance by reducing sexual harassment in damselflies. *Nat Commun* 5:4468.
- Voigt C, Goymann W. 2007. Sex-role reversal is reflected in the brain of African black coucals (*Centropus grillii*). *Dev Neurobiol* 67:1560–73.
- West-Eberhard MJ. 2003. Developmental plasticity and evolution. New York: Oxford University Press.
- Westrick SE, Moss JB, Fischer EK. 2022. Who cares? An integrative approach to understanding the evolution of behavioural plasticity in parental care. *Anim Behav*. (<https://doi.org/10.1016/j.anbehav.2022.10.005>).
- Willink B, Duryea MC, Svensson EI. 2019. Macroevolutionary origin and adaptive function of a polymorphic female signal involved in sexual conflict. *Am Nat* 194:707–24.