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SYMPOSIUM ARTICLE

It Takes Two to Tango: Including a Female Perspective in Reproductive Biology

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Synopsis Like many scientific disciplines, the field of reproductive biology is subject to biases in terminology and research foci. For example, females are often described as coy and passive players in reproductive behaviors and are termed "promiscuous" if they engage in extra-pair copulations. Males on the other hand are viewed as actively holding territories and fighting with other males. Males are termed "multiply mating" if they mate with multiple females. Similarly, textbooks often illustrate meiosis as it occurs in males but not females. This edition of Integrative and Comparative Biology (ICB) includes a series of papers that focus on reproduction from the female perspective. These papers represent a subset of the work presented in our symposium and complementary sessions on female reproductive biology. In this round table discussion, we use a question and answer format to leverage the diverse perspectives and voices involved with the symposium in an exploration of theoretical, cultural, pedagogical, and scientific issues related to the study of female biology. We hope this dialog will provide a stepping-stone toward moving reproductive science and teaching to a more inclusive and objective framework.

Introduction

Although human pregnancy and lactation are well-studied, within the broad research area of reproduction across taxa, female biology has remained largely understudied and sometimes outright ignored. Often research questions have been investigated from a female-passive, male-active framework, and often studies have used male biology as the baseline from which to investigate female biology. However, evolutionary pressures driven by natural and sexual

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selection are just as capable of influencing female traits as they are male traits, including aspects of neurobiology, physiology, behavior, morphology, and ecology, all of which are critical for individual survival and reproductive success, regardless of biological sex. The preceding set of manuscripts in this volume makes strides by synthesizing new developments, by refining language to remove bias, and by considering and using experimental designs to enhance our understanding of female reproductive biology.

Here we address numerous questions that came up during our symposium. These are grouped by theme. We start with theoretical issues of perspective, then move to cultural influences on how studies have been done. We conclude by discussing pedagogical issues around the female perspective and by highlighting the exciting research advances that may occur when the biases of traditional assumptions are removed.

Reproductive biology, like many other scientific fields, lags behind changes in our social and cultural climate. This lag is evident in conceptual paradigms, in pedagogy, in language, in peer review, and in research foci. We use an informal question–answer format to discuss these topics and to help make researchers cognizant of potential theoretical, linguistic, and research issues. We hope this dialogue continues and promotes future insights into poorly understood or poorly investigated aspects of female biology.

Theoretical: what, why, examples, implications

Many theoretical issues surround the study of female reproduction both at present and historically. First, we define what we mean when we refer to the female perspective. We then address the many ways taking this perspective may change both how we conduct science as well as the conclusions we reach. We conclude by emphasizing that studying both sexes is important.

What is the female perspective?

Here are four different views of the female perspective.

T.J.O.: The female perspective is the stance taken by researchers when the female is placed as the focal and active sex for a given inquiry.

K.A.H.: The female perspective is a means for correcting an inherent bias in our literature and in our language as scientists that assumes females are secondary and males are primary. Although we are currently discussing it in the context of reproductive biology, it is important for us to understand and consider the female perspective within the scientific community as a whole.

C.C.J.: To me, the female perspective encompasses the above definitions and focuses on understanding females relative to themselves, rather than understanding females relative to their male conspecifics. We do not need to explain our results from investigations in females within the same framework as males. Understanding female physiology is interesting in itself, without necessarily having to be related back to males as a reference point. Small semantic difference, but the change in emphasis (in my opinion) affords the opportunity to shift from testing hypotheses largely based on males to hypotheses informed by female reproductive biology.

L.K.S.: As an evolutionary and behavioral biologist, I think of the female perspective as considering and evaluating alternative hypotheses for how female phenotypic traits have evolved, in the style of earlier leaders in this field including Jeanne Altmann, Kay Holekamp, Sarah Blaffer Hrdy, and Barb Smuts.

Why the female perspective? What are some of the issues?

Key issues arise when the female perspective is not taken. We explore these issues by drawing examples from anatomy, behavior, physiology, neurobiology, and immunology.

V.H.: Historically the formal study (and teaching) of reproductive biology has been the purview of men. Women doubtless shared information about their bodies as well as about pregnancy and lactation, but this knowledge was not codified in any formal manner. Thus, formal knowledge of reproduction was generally presented from the male perspective. This bias persists in current terminology, concepts, and theoretical frameworks. For instance, "In describing *meiosis*, the process by which diploid cells are converted into haploid cells, every introductory biology textbook that I have ever seen describes the process that occurs in males but omits any description or even mention of meiosis in females" (Gorelick 2012, 623). You can do your own test by searching Google images for "meiosis" and seeing what proportion of images show polar bodies (a characteristic of female meiosis). Try a search for "female meiosis" and you will find that a number of images also include spermatogenesis.

A.A.K.: Despite "calls to action," in the last decade suggesting that more studies include both sexes and/or emphasize mechanisms of female reproduction

(Ball and Ketterson 2008; Caro 2012; Shansky 2019), a sex-bias favoring males in the field persists, as demonstrated by a literature investigation across avian taxa. Males are often thought to be easier to study because (1) males are easier to observe or catch for sampling in the field, as they are often defending a territory and have more flashy visual or vocal signals and (2) females are less likely to breed in captivity, especially in birds (Caro 2012). While there might be some different challenges associated with studying physiological mechanisms in females and males, there are also efficient solutions to these challenges, such as shifting the focus of observations to females and using hormone manipulations to adjust female responsiveness in captivity (Caro 2012). Therefore, a lot of this persistent bias can be explained by the outdated standard established by the field and its underlying misconception that female physiology is more complicated than that of males (Shansky 2019).

T.J.O.: In the area of morphology, female anatomy has been much less documented than that of males. The best example of this is of the glans clitoris versus its homolog in males the glans penis. Another example is that of sperm storage in many vertebrates, for which the female's anatomy and functions have only been dissected in a few species, and by a small number of labs. In many reproductive processes, sperm or other male contributions are often described as active players while the role of the female has been less studied and often under-emphasized.

A.K.L.: In addition to the glans clitoris and glans penis, another example of biased anatomical knowledge is the prostate. Textbooks, diagrams, or peer-reviewed publications do not ignore the male prostate. However, the female prostate, also referred to as the Skene's gland, is sorely overlooked and lacking in textbooks, diagrams, and peer-reviewed publications. This organ is significantly understudied and is even missing from Gray's Anatomy. A quick PubMed search exemplifies this inequality: while "male prostate" has 155,871 search results, "female prostate" has 22,559 and "Skene's gland" has just 49. This bias is particularly interesting because the Skene's gland is responsible for ejaculation and often considered to be a determining factor in orgasm, but we know relatively little about it.

V.H.: Further evidence of the greater emphasis on male anatomy is provided in the Terminologica Anatomical [terminologia-anatomica.org/en] in which fewer terms are provided for aspects of female anatomy than for males.

S.E.L.: I work on a group of birds that are celebrated as an example of the female perspective in sexual selection: female jacanas face stronger competition for mating opportunities than males, a pattern known as "sex-role reversal." Despite its intended meaning to point out a rare pattern (Kokko et al. 2013), this term that is loaded for several cultural and biological reasons (Ah-King and Ahnesjo 2013; Amundsen 2018). First, "sex roles" imply that there is a suite of prescribed roles for females and males in each species, which often assumes that females are caring and choosy, and males are competitive. So, sex-role reversed species should have competitive females, and caring and choosy males, right? Not quite. In jacanas, males conduct the majority of parental care, but females and males competitively defend their breeding territories, and both sexes have weapons (wing-spurs). It is assumed that males are choosy, but in fact, we know very little about mate choice in jacanas. Lumping together competitive behaviors, parental care, mate choice, and so on as prescribed sex roles breaks down when we consider that these behaviors are often independent of one another. For example, in bony fishes, stronger sexual selection on females is found only in a few species like pipefish, yet male-only parental care is widespread (Benun Sutin and Wilson 2019). A second problem with the term "sex-role reversal" is its categorization of females and males into a binary. Variation in competitive and parental phenotypes (within and among individuals and species) is continuous, rather than dichotomous. A third issue is that the term "sex-role reversal" positions males as the central, normative expectation, and considers females relative to the male condition: competitive females are considered "male-like," though there is nothing male about them. The more we study females for their own sake, the more opportunities we have to learn why the evolution of competitive traits in females makes sense, instead of why they are paradoxical.

K.H.: Continuing my role in recalling intellectual history, one fundamental binary in diploids is "the Fisher condition" that one female and one male gamete are needed for each zygote—huge consequences follow. Identifying "caring vs competing" as expected "sex roles" goes back to Darwin (1859). He introduced his theory of sexual selection in the Origin to explain how male "armaments and ornaments" that interfere with likely survival could persist—be adaptive—because they served male mating success. In part II of the Descent (Sexual Selection) he said,

> When the two sexes differ in structure in relation to different habits of life ... they have no doubt been modified through natural selection.... So

> …the primary sexual organs, and those for nourishing or protecting the young, come under this same head: for those individuals which generated and nourished their offspring best, would leave, ceteris paribus, the greatest number to inherit their superiority; whilst those which generated or nourished their offspring badly, would leave but few to inherit their weaker powers (Darwin 1871, 256).

Other differences between the sexes, such as male armaments and ornaments, cannot be explained by "ordinary" natural selection, because:

> the males have acquired their present structure, not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males…. That these characteristics are the result of sexual selection and not of ordinary selection is clear, as unarmed, unornamented, or unattractive males would succeed equally well in the battle for life and in leaving numerous progeny, if better endowed males were not present (Darwin 1871, 258).

Recent proposals that use the label "sexual selection" to refer to differences between the sexes in competition over things other than conceptions obscure Darwin's fundamental insights about the distinctive consequences of mating competition. Most primate females are extremely competitive over food, and as Sarah Hrdy (1986) has noted so eloquently, our own primate order—full of libidinous females, actively seeking copulations with multiple males—should have overthrown the textbook characterizations of females as "coy" long ago. But primate females who are actively seeking copulations are not usually competing for conceptions but being "assiduously maternal" (Hrdy 1999, 87, 88). The adaptive benefit for copulating with multiple males comes from spreading the possibility of paternity, which reduces the danger of male infanticide, thus increasing offspring welfare (Hrdy 1981, 1986, 1999). Just as female primates soliciting copulations may not be an outcome of sexual selection in Darwin's classic sense, "care" that appears to be parenting may be maintained by mating competition instead. Darwin himself puzzled over egg guarding in teleost fish. Although often labeled "paternal care" (mentioned by Benun Sutton and Wilson 2019 cited above), that label ignores an alternative sexual selection hypothesis: defending a desirable egg laying territory from other males gets the defender more paternities.

K.A.H.: Historically, our understanding of gametes began with an observation of sperm cells by Antoni van Leeuwenhoek in 1677 (Birkhead and Montgomerie 2009). It was not until 1841 that sperm were recognized as cells, and it would take another 20 years for ova to be recognized as cells by Karl Gegenbaur (Birkhead and Montgomerie 2009). This lag in our understanding of female biology may reflect the technology available at the time that limited scientists to describing only what they could see, and an ejaculate is necessarily easier to see than an ovum. However, a lag in understanding female biology continued to persist centuries later. Darwin described sexual selection in 1871, and nearly a century later, Geoff Parker pioneered an entirely new field of study when he wrote about "sperm competition" in 1970. In this seminal article, he described ways in which males compete at the level of their gametes to reach and fuse with ova—analogous to the male competition envisioned by Darwin prior to mating. However, Darwin also envisioned another mechanism that generates differential reproductive success among individuals—female choice. In a review on post-copulatory sexual selection, Tim BIrkhead and Tommaso Pizzari (2002, 266) write:

> …the idea that females had an active role in sexual selection was historically regarded with some scepticism, as was the idea that females actively chose their copulation partners and solicited copulations from several males. A cultural bias therefore discouraged an initial interest in cryptic female choice. Although first proposed in 1983 [by Thornhill], the catalyst for the current interest in cryptic female choice was the extensive review by Eberhard, which explored the potential mechanisms that females could adopt to bias sperm storage and use in favour of certain males and against others.

Bill Eberhard's book on "female control" was published in 1996, a quarter century after Parker's "sperm competition" paper. While better late than never, the question remains—why so much later? It is a question that we may still ask in 2020. A quick perusal through Google Scholar for the search term "sperm competition" yields 34,400 results, yet a search for "cryptic female choice" yields 6160 results (Fig. 1a). One could argue that the 26-year lead of sperm competition studies is what drives these enormous differences. Yet when we just look at just the published record for 2019, those results are 1270 and 310, respectively (Fig. 1b). In both cases, studies from the female perspective in post-copulatory sexual selection represent <20% of our research output. It is this persistent and historical bias in the literature that demonstrates why there is such a need for

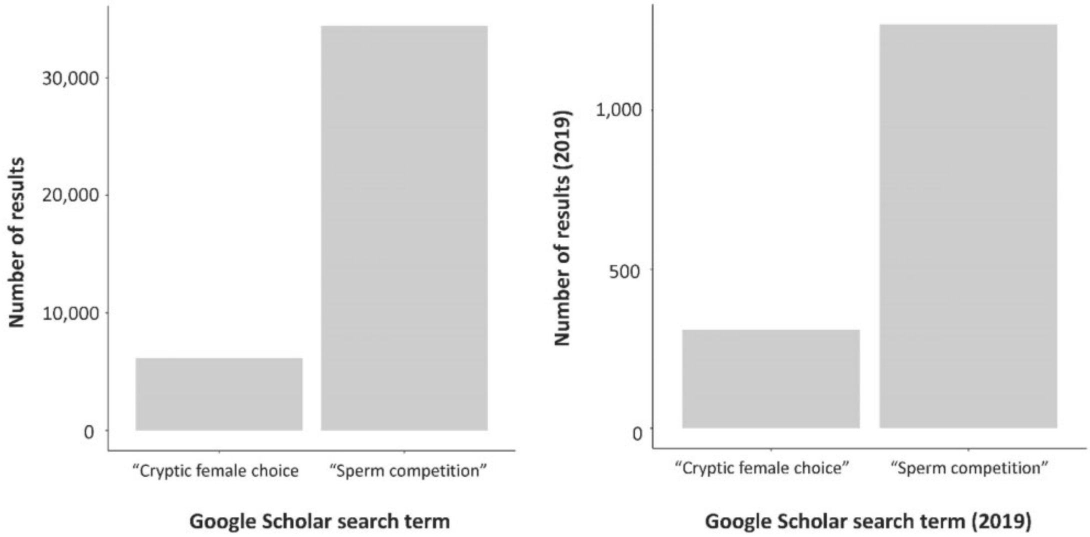

Fig. 1. Results from a Google Scholar search for research articles in the field of post-copulatory sexual selection. "Cryptic female choice" studies concern female traits that allow them to control sperm use, whereas "sperm competition" studies concern male traits that allow them to outcompete one another at the level of their gametes after mating. Both overall search results (**a**) and search results restricted to just studies from 2019 (**b**) reveal a significantly smaller number of "cryptic female choice" articles compared to "sperm competition" articles (from Kristin Hook).

us to shift our focus to the female perspective so that we may begin to shed light on female reproductive traits driven by post-copulatory sexual selection.

K.S.L.: Understanding the female perspective on reproduction also requires a comprehensive understanding of the neural architecture underlying the female "reproductive" brain. By defining the neural-, molecular-, and hormonal-basis of reproduction in females, we may be able to understand how the nervous system integrates information in the female brain and the underlying psychology of females in reproductive contexts. Unfortunately, males frequently serve as the model in which to understand the molecular and neurobiological basis of reproduction. This is largely due to physiology, as hormonal fluctuations are a critical component in both appetitive and consummatory aspects of reproduction and these are much easier to track in males relative to females.

V.H.: But don't we have a contradiction here? If hormonal fluctuations are critical, then shouldn't one study females because their hormones fluctuate with predictable regularity.

C.C.J.: Much of the discipline of ecological immunology (ecoimmunology) is derived from sexual selection theory (e.g., Hamilton and Zuk 1982; Folstad and Karter 1992), and thus males have been the focus of investigations. Empirical results from the few studies on females are often interpreted within the context of previous findings in males. Despite the large amount of anthropological and biomedical evidence that female and male immune systems are different (Klein 2000; Ngo et al. 2014), potentially due to differences in shared pathways and/or fitness effects. the relationship between reproduction and immune defense lacks a unified framework for females.

M.B.: Historically, taxonomic work on Arthropoda has relied heavily on male reproductive morphology and behavior due to ease of access as well as the assumption that female choice drives diversification of male reproductive traits while females remain static (Ah-King et al. 2014). My work with Opiliones has challenged this assumption (Burns et al. 2013; Burns and Shultz 2015), and many workers have adopted technologies such as microCT (Mattei et al. 2015), electron microscopy (e.g., Wortham-Neal 2002; Grodowitz et al. 2019), and fluorescent microscopy (Fitzer et al. 2012) for elucidation of internal structures in females. However, the assumption of female morphological invariance seems to persist.

L.K.S.: I would urge a holistic approach to studying reproductive behavior from an evolutionary perspective. Individual organisms operate within a system of interactions with conspecifics, heterospecifics, and their abiotic environment. Often times, the benefits and costs of particular behavior can be understood only when considered, at the very least, across an individual's lifetime and, better yet, across multiple generations. Any studies of the evolution of reproductive behavior in sexually reproducing organisms that do not consider the roles of, and costs and benefits to, both sexes are going to be necessarily incomplete and will likely lead to erroneous conclusions.

Are there areas where our perceptions would change if we took the female perspective?

Yes. We identify four specific areas in which a change of perspective will greatly impact our conclusions: social behavior, mate choice, postcopulatory sexual selection, and the study of evolution with respect to cooperation and trade-offs.

V.H.: Yes. Here is an example from mammalian social behavior. Although mother–offspring bonds are inherently social, and mothers spend much of their lives with offspring and not alone, these interactions are not considered evidence of sociality for the species. For instance, a recent Mammal-L listserver comment on a video of brown bears stated: "Either these bears are more social than I thought, or it is a female with three yearlings." The implicit assumption was that interactions between females and yearlings do not qualify as social behavior. If female interactions with yearlings are excluded as evidence of sociality, then what do we mean by sociality?

T.J.O.: Certainly. If females are seen as only minor contributors to complex traits like female sperm storage this means we are making assumptions that the male is responsible for driving this phenomenon through the production of sperm with certain morphologies and an ejaculate with a certain composition. However, if instead we see this as a cooperative process we may study what both sexes contribute, how females control where sperm are stored and how females orchestrate their use of sperm and the timing of that use.

KAH: Absolutely. It is often taken for granted in studies of post-copulatory sexual selection that observed biases in sperm use are driven by male sperm competition. However, there is evidence in a weevil that sperm precedence patterns change when muscles within the female sperm storage organ are experimentally severed (Villavaso 1975), signifying that females play an active role in sperm storage and use. This active female role was also demonstrated in fruit flies when Mollie Manier et al. (2010) designed a clever experiment to directly observe sperm motility, storage, and use directly within the female reproductive tract. Taking the female perspective into account, that study changed the way we think about the interaction between females and the ejaculate after mating and the importance of considering the dynamic processes occurring within the female during and after sperm transfer within internally fertilizing species. Another recent study in the house mouse contributed to our understanding of these active female processes as well, showing that there are wavelike muscular contractions within the female oviduct that alter the movement of sperm (Ishikawa et al. 2016).

K.S.L.: Female mate-choice is one of the most consequential decisions that a female will make in her lifetime. A female's decisions about whom to mate with and whom to reject are made when she experiences a unique blend of social contexts and physiological conditions. To date, it has not been well-appreciated how this unique blend of social and physiological conditions can provide an important glimpse into the neural basis of decision-making processes. Decision-making does not occur in static conditions. Rather, it occurs across environmental, social, and physiological conditions; all of which have the potential to influence the outcome of the decision. Thus, if we accept the female perspective during appetitive aspects of reproduction, we would be able to develop new and exciting models for decision-making, especially as it occurs during a fluctuating physiological background. The acceptance that females are the decisive sex during sexual encounters allows us to move into molecular, physiological, and neurobiological studies with the aim of understanding the psychology of decision-making that occurs during specific social and physical conditions.

V.H.: Yes. An additional complication is that females may solicit copulation for reasons other than the production of offspring, especially in some primate societies. A related example is the femme fatale fireflies (*Photuris*) that solicit males in order to kill and eat them.

M.B.: Application of new technologies to visualize female reproductive morphology and internal physiology (Mancini and Pensabene 2019) could lead to entirely new observations and hypothesis on the evolutionary mechanisms for diversification in animals. For example, if females are understudied, coevolutionary arms races might not be identified (Perry et al. 2017).

L.K.S.: Yes. In the investigation of seminal fluid molecules, the female perspective could really alter both the phrasing that is used to talk about the processes involved and the conclusions that are drawn about the fitness consequences to both sexes. For example, many researchers have considered mostly the role of males in the evolution of these molecules and "manipulation" of female behavior and physiology. Some notable exceptions who have been leaders in considering the female role in the evolution of seminal fluid molecules include Mariana Wolfner (see below), Bill Eberhard, and Carlos Cordero.

K.H.: Cooperation can be important, sometimes interests overlap but they rarely overlap perfectly. One benefit of an evolutionary perspective is recognizing that conflicts of fitness interest are everywhere, including between mothers and offspring, and including sexual conflicts between females and males. Different fitness-related tradeoffs for each player contribute to the complexity of social life.

Has all reproductive biology ignored the female perspective?

No. Here we identify several fields of study where the female perspective has been the focus of research: life history theory, mate choice, mitochondrial DNA, animal production science, and primate social structure.

T.J.O.: Certainly not. In fact, early works in the area of life history theory largely ignored males. This is for a variety of reasons such as that female contributions to parental care are easier to observe, that maternity in many taxa is easily assigned, and that in some cases a focus on one sex simplified mathematical models.

K.A.H.: Eberhard's book on "female control" of sperm use did just the opposite by focusing on potential mechanisms of cryptic female choice and providing an extensive review of empirical evidence across taxa. Subsequent to its publication, there have been a trail of studies attempting to elucidate this phenomenon, including a clever experiment in mice by Renée Firman and Leigh Simmons in 2013 that showed the capacity of the female gamete to strategically adjust its ability for conception when females choose to mate with multiple males.

K.S.L.: One aspect of reproduction in which females have received the bulk of attention is in understanding both the ultimate and proximate mechanisms of mate choice or mate preference; appetitive components of reproduction. It has become abundantly clear that in most systems, female mate choice drives the evolution of male courtship and mating strategies, indicating that females are in the driver's seat during reproduction. And yet, historically the view that females (1) limit male reproductive opportunities, (2) pace male mating behavior, and (3) are exceptionally selective about whom to mate with during reproduction has been met with some trepidation (see remarks about Darwin above).

In the last few decades, emphasis on perceptual and cognitive biases of females has slowly progressed us toward an acceptance and understanding of the psychology of females in reproductive contexts. Defining the psychology of females during mate choice reveals that males are the ones scrambling, in an evolutionary sense, to evolve traits that will match the female's aesthetic sense or her taste for the beautiful (Rosenthal 2017; Ryan 2018). Through studies of the female mind regarding mate choice, we are now poised to redefine the female's role in sexual encounters. Females are not passive during reproductive encounters; rather they often seek sexual encounters. Thus, females should be considered proceptive actors in all sexual encounters rather than being receptive to male stimuli.

V.H.: In addition, studies that use mitochondrial DNA as an evidentiary tool are focused only on maternal inheritance. More obviously, studies of ovulation, gestation, and lactation clearly focus on female reproduction.

A.A.K.: Studies on mechanisms of reproduction in poultry and animal science, large animal veterinary medicine, and similar fields have focused on a female perspective. Many studies in this field are investigating how to increase the productivity of food resources, which is largely driven by females, whether that is reproductive performance (e.g., offspring for meat industry) or production of byproducts (e.g., milk and eggs).

L.K.S.: Certainly not. In the field of reproductive behavior, female primatologists in the 1960s and 1970s, for example, were instrumental in revising and filling in our understanding of primate social systems, including the reproductive decision making of females.

Should we stop studying males?

No. We must continue to study both females and males. Below we provide 8 reasons why we need to study both sexes equally even if up until now females have been understudied.

K.A.H.: No. We are merely saying that female reproductive traits are just as important to study as male reproductive traits are. They often co-evolve, and we understand very little as scientists by focusing on only one side of the coin when the odds depend on both sides.

T.J.O.: Of course not. In no way are we suggesting that we cease studying males, nor that we only study female reproductive biology. Readers are discouraged from making this jump in logic as such a proposition is missing the point of our premise in this article. In fact, many of us (this piece and edition) are interested in how traits evolve for reproductive success and this necessitates the inclusion of all players; mother, offspring, father, and non-kin.

We also must avoid the argument that because some researchers focus on the female perspective they all do (and thus there is no problem). Indeed, the ideas we outline here have not been entirely ignored by all scientists (e.g., see our discussion of life-history evolution) but writ-large are issues resulting from a bias toward males are pervasive in the field.

S.E.L.: Studying the reproductive biology of both female and male animals can reveal the many diverse ways in which nature builds phenotypes. Sometimes the sexes converge to express similar behavioral phenotypes, like aggression, but have divergent underlying physiological mechanisms that produce those phenotypes, for instance, different levels of testosterone in circulation.

K.H.: .... and "all players" can include more than "mother, offspring, and father," not only because competition for paternities can shape phenotypes. There is also sibling rivalry, and, in our lineage, grandmothers. More generally, depending on the taxon, inclusive fitness effects likely contribute to reproductive phenotypes.

K.E.H.: Killer whales (*Orcinus*) and elephants (*Elephas, Loxodonta*) are other long-lived taxa for which grandmothering may apply .

K.S.L.: No one is suggesting that we stop studying males. As Lehrman (1961) suggested decades ago, the interactions between females and males are just as necessary during the appetitive components of reproduction as they are during the consummatory aspects of reproduction. Thus, it is nearly impossible to interpret the behavior and physiology of females during reproduction if we do not consider the male contribution. However, we acknowledge that our understanding of nearly all aspects of reproduction are lagging in females when we compare it to what we know about males. This symposium and the corresponding papers are a call to address this issue.

A.K.L.: Of course not. No one is suggesting that we stop studying males. What we are advocating for is to invest in studying females. With regards to embryonic development, we know relatively little about the development of the vagina, clitoris, and Skene's gland compared to what we know about penis and prostate development.

A.A.K.: In the field of physiological mechanisms of reproduction, it is important to understand sex differences in the mechanisms of reproductive timing and function in order to determine the evolutionary consequences. You cannot understand sex differences if you are only studying one sex. But in cases in which researchers are limited, and can only study one sex, I think an emphasis should be placed on females because we are lagging behind on research focused on female mechanisms. Also, female reproductive timing and output arguably have stronger evolutionary consequences on both females and males, as they determine the timing of breeding and the number of offspring produced (Williams 2012).

Cultural influences and consequences

Here we dive into aspects of our culture that impede using the female perspective in research. The issues include: time lags, traditional cultural expectations, economic and social disparities, popular versus scientific language, and the process of peer review.

Why do changes in science and associated terminology not keep step with cultural changes?

While the study of how culture impacts science is a field onto itself, here we provide our views of some reasons behind the slow embrace of the female perspective in both basic and applied research.

K.A.H.: Just because we recognize a problem does not mean we can solve it immediately. Women are still paid less than men. Women are more likely to leave academia, and they represent a smaller proportion of tenured professors than men. These kinds of inequalities seep down into other aspects of science, including what research gets done, is perceived as interesting, or gets funded. I believe we must simultaneously address these issues regarding diversity, equity, and inclusion if we want to advance the scientific enterprise.

T.J.O.: The standing views held by the scientific community change slowly. By the time this article is published, 100 years will have passed since women in the USA were granted the right to vote (legislation 1919, first voting in August 1920). During those 100 years, the political and social influence of women in commerce, public service, and entertainment has significantly increased. Until recently, most doctors, scientists, professors, and researchers have been men, and most cell, animal, and human study-subjects have been also male (https://theswaddle.com/research-sexism-has-always-colored-health-care-to-the-point-of-keeping-women-unhealthy/) even in studies about female biology. An extreme example, as mentioned by Maya Dusenbery in "Doing Harm," is a pilot study, supported by the National Institute of Health(NIH), that explored the effect of obesity on breast and uterine cancer, but did not enroll a single woman (Dusenbery 2018).

By the 1980s, women scientists organized and advocated for Congress to include women in clinical trials. Their efforts resulted in a 1985 report on women's health and, after another 8 years, in 1993, the NIH and the US Food and Drug Administration required that women be included in clinical trials (NIH Guide 1994). However, not until 2016 (NIH Guide Notice 2015) did NIH mandate that female animals must be included in pre-clinical trials, for example, laboratory rodent studies (Miller et al. 2017).

Although some major government funding institutions have recognized that female biology is relevant to both females and males, most current scientific research still operates within the norms of past centuries, in which male biology is the template and female biology is the exception. While medical science is making slow advances, comparative physiology, for the most part, often still assumes that understanding male biology is sufficient.

K.H.: Such a vexing question, especially these days. Should not our ready access to information get us all on the same page? Scientists have trouble keeping up in their own specialties, and more and more specialization builds new silos. We cannot use language, but jargon makes communication harder. We want to use words that wider audiences will understand, yet meanings can and do shift and diverge. Time taken to trace and explain ideas and lines of evidence, not only involves choices about "which history" to trace, that time trades off against whatever is the story at hand.

L.K.S.: I think it can actually go both ways. Sometimes, science advances faster than cultural, ethical, and moral considerations can keep pace. In contrast, science and science education can lag in keeping up with cultural challenges to orthodoxy. For example, broadly-speaking, the scientific study and teaching of reproductive biology has not reflected the current state of cultural considerations of gender fluidity. Why are we slow to change? I think that it takes a new generation of scientists to become the leaders and teachers in the field and to spread the new cultural considerations into our field—so that these considerations are the expectations and not the exceptions.

V.H.: We have known that the concept of a "sperm race" was debunked >70 years ago, why has not that myth disappeared?

S.E.L.: I think this has a lot to do with popular depictions of science in the media. When videos, cartoons, and memes are funny AND informed by science, their educational reach is powerful. The more we as biologists can pair with science communicators, the more effective our translation of research will be. One of my favorite SciComm videos tells the herstory of the clitoris, by Lori Malepart-Traversy: https://vimeo.com/222111805. It is short, amusing, and addresses a lot of misconceptions in clever ways.

K.H.: Thank you Sara! What a treat!

Can the peer-review process help?

Peer review has many benefits and is becoming ever more refined such as including double-blind manuscript assignments. However, peer-review remains an imperfect system for major social changes in the sciences.

V.H.: Unfortunately, the peer-review process also slows progress, because scientific "peers" are not always cultural "peers." Although "peers" may be in the same scientific discipline as the research being reviewed, such peers are often from higher academic ranks and may have inherited cultural biases. In addition, the choice of reviewers is often part of a social networking process. Peer review by older and more traditional-value holding colleagues may discourage changes both to language and to well-regarded theories and methodologies. Younger colleagues, who are still working toward tenure or other advancement, may be reluctant to use gender-neutral, but less familiar, terms such as "gamete fusion" instead of "fertilization" for fear their manuscripts or grant proposals may be rejected. Thus, changes in language, methodology, and conceptual paradigms are impeded when the evaluation process for grants and manuscripts is biased against changing "normal" practice or assumptions.

A.A.K.: We hope by drawing more attention to this problem in the literature, we will inspire more of our peers to use and encourage use of gender-neutral terms as well as to consider the female perspective when reviewing manuscripts and grant proposals.

K.A.H.: Unfortunately, cultural biases are tenacious and ubiquitous, so peer-review will only work so long as everybody is on board and willing to adapt to the changing norms.

L.K.S: In addition to what the others have said, I think that journals could establish best practices and principles for peer review that reviewers are asked to agree to. These principles and practices could include applying standards for evidence equally across female- and male-mediated processes. For example, I had the unfortunate experience of having a reviewer require that I remove my claim that data supported the hypothesis of "cryptic female choice" when my evidence was much stronger than much of the evidence presented in papers that claim to have demonstrated "sperm competition."

A.A.K.: I recently received a review on a paper criticizing the fact that I measured testosterone (T) in females. When I briefly defended that T played an important role in females and that it entered circulation, the reviewer responded very positively.

Pedagogy and the female perspective

With ever improving standards for teaching we are often asked to incorporate our research with our teaching. Here we discuss how our understanding of the female perspective informs our teaching. Readers may note that this section yielded among the most diverse responses in this entire manuscript.

How do these factors impact teaching? Ex: often I get asked if the female is the "default" sex, since males will develop in response to testosterone in humans. I hate this terminology, but do not have a good answer.

This question from the audience generated a diverse set of answers.

V.H.: I agree this is a problem. For example, Wikipedia's description XY sex-determination said "'Female' is the default sex" [https://en.wikipedia.org/wiki/XY_sex-determination_system, accessed 15 March 2020].

S.E.L.: In mammalian sex determination, there is no "default state"—testes and ovaries develop from a bipotential gonad—this is an active, gene-directed process (Gilbert 2000).

M.F.W.: I think that some of the reason that females were considered the "default" came from experiments like Alfred Jost's in the 1950–1960s, in which removal of gonads from rabbit fetuses before sex differentiation led to female development of the fetuses (reviewed in Jost 1970). But (in addition to lacking gonads and thus hormones of their own) those fetuses developed within a female rabbit, subjected to her female hormonal milieu, which affected their own sex development.

S.E.L.: There is also a misconception that testosterone is a "male hormone." Females also have functional levels of testosterone, though often (but not always) at lower levels in circulation than in males.

M.B.: Just wanted to throw in here that, just as sex determination follows both genetic and environmental pathways as is ably explained above, variation abounds even within these categories. In ZZ/ZW systems, the W-chromosome (present in females), does not have a locus of female determination, but instead dosage of genes like DMRT1 has been suggested as the major switch for sex (Ezaz et al. 2006). Considering haplodiploid systems (as in Hymenoptera), it might indeed be accurate to call males the "default sex," as they develop from haploid ova in a process called arrhenotoky (Goudie and Oldroyd 2018). In systems with temperature-dependent sex determination, different temperature regimes can produce different resultant sex ratios, even within a single population (Refsnider and Janzen 2016).

A.A.K.: While estradiol (i.e., E2) is often considered the primary "female hormone," testosterone is the precursor to E2. Vertebrate ovaries also secrete testosterone into the circulation (Staub and DeBeer 1997; Ketterson et al. 2005; Goymann and Wingfield 2014; George and Rosvall 2018).

N.L.S.: Yes, there are a lot of examples of androgens playing a normal role in female development (see Staub and DeBeer 1997 for a review) and of estrogens playing a normal role in male development. Students are fascinated to learn about specific examples that expose these misconceptions about "female" and "male" hormones. For example, estradiol is critical in spermatogenesis. Examining the role of the traditional "sex" hormones in both sexes holds a lot of promise.

L.K.S.: I think that the sections on evolution of reproductive biology and behavior in many introductory textbooks should be revised to be more sex-neutral and gender-inclusive. Project Biodiversify (projectbiodiversify.org) has an excellent workshop and teaching materials on this topic.

V.H.: The introduction to this symposium volume includes a table of gender-neutral terms and suggestions for less biased figures and phrasing (Orr and Hayssen 2020).

How does the female perspective influence your teaching?

The variety of ways we have incorporated the female perspective is highlighted here. They focus on challenging our students to think carefully and critically about biases in the field and to make this awareness part of the classroom culture. Two comments at the end discuss some specifics with respect to timing and content.

V.H.: I teach first year students at a women's college. At the beginning of the semester, they all believe that sperm race to the site of conception and that a menstrual cycle is 28 days. These misconceptions may have profound consequences on their understanding not only of basic reproductive biology, but also of their own reproductive biology. The female-passive, male-active myth is part of the cultural ethos and permeates biological education.

T.J.O.: Aside from general frustrations with textbooks that neglect females or, when including them, write them as passive players, I am usually excited to find that students are happy to embrace change and ask questions that are not bound by historical conventions. As a result my teaching links to my research nicely and allows me to help ensure that future biologists are willing to challenge the status quo.

A.A.K.: Addressing student misconceptions is one of the pillars of pedagogical research on student-centered learning (Sewell 2002). Since students enter the classroom with prior knowledge and beliefs, instructors should address misconceptions head-on to avoid students choosing to reject new information (Sewell 2002). As an example, my colleague set up a lesson on mating systems by identifying misconceptions (e.g., females are passive while males are territorial and aggressive) and then using data that debunked the misconception (e.g., female tree swallows are territorial over nesting sites).

In addition, instructors should keep up with the literature. This symposium shows that many scientists are thinking AND publishing on these ideas. It is important to use examples from the "female perspective," so that students do not see females as the passive sex.

It is also important that instructors are conscious about word choice and examples used in the classroom to avoid the male bias. Even as a feminist who studies female reproduction, I have been caught using gendered "relatable" examples when talking about parental care. I did not even notice that I had until I had an observer in the classroom give me feedback!

K.H.: Young females seem an especially important audience for reproductive biology because concerns about youthful appearance and physical fitness in popular culture converge on obscuring human life history. First year students, likely not yet 20, will remain healthy and productive long past the end of their fertility, which ends in women about the same age it ends in female great apes. But, as Jane Goodall said for chimpanzees at Gombe, they become "aged" by 33, and usually die while they are still cycling. Humans *age much more slowly* than chimpanzees . Even though average age at first birth keeps increasing in the USA—for good economic reasons—that does not delay menopause.

D.J.S.: A recurrent question in teaching as well as in research is when to reduce and when to embrace complexity. Continuing with our earlier example, one interpretation of the modern history of the female as default paradigm for gonadal sex determination is that it was motivated by pursuit of a simple master switch model of developmental genetics with single points of control (Fausto-Sterling 1989). When a candidate was found in the testis-determining factor *SRY*, the perceived elegance of the model and its fit with background cultural assumptions of males as dominant made it alluring and it caught on. Reality, of course, turns out to be more complex, and even if a protein promotes testis development and inhibits ovarian pathways, that does not mean that ovarian identity lacks its own active developmental process (Eicher and Washburn 1986; Edson et al. 2009); in fact, mutual antagonism of alternative identities, from cell types to organs, is an ubiquitous aspect of development, and gonads are no exception. This position is echoed in a recent developmental biology textbook (Gilbert and Barresi 2016, 187; see also Hayssen and Orr 2017, 31) which presents a more symmetrical alternative to the male-dominant model. In this case teaching the more holistic model helps avoid perpetuating stereotypes students may come in with, something certainly important enough to be "worth" the added complexity.

Comparative biology is a powerful way for students to challenge preconceptions by identifying counterexamples and caveats. For instance, the vast diversity of vertebrate sex systems, such as temperature- and behavior-dependent sex determination, and the chromosomal system in birds where females are the heterogametic sex, make the female as default paradigm untenable in greater context (Crews 1993), and show that the apparent dominant effect of *SRY* is but one lineage's mechanism (Graves and Shetty 2001). Scientific debates between female and male perspectives on sex determination show how background assumptions shape the interpretation of scientific findings (the all-important step between "results" and "discussion"). Perhaps examples like this can be used in teaching to help students move from acceptance of textbook knowledge as established fact to critical reading of the literature.

K.S.L.: Teaching sexual selection via mate choice can be tricky at the undergraduate level. Even when the example used in class is clearly a nonprimate system, students often want to apply the behavior to their own behavior. Typically, a discussion ensues about male mate choice and its importance in human behavior, which often clouds the concept I am attempting to discuss with my students when teaching mate choice in frogs, fish, birds, or any other nonhuman system.

K.A.H.: I think it is very important to bring up and discuss these issues at the very beginning of the semester to provide a historical overview, highlight the bias in the field, and humanize the scientists whose work they will be reading about. Then throughout the semester, you can point out these biases when you come across them. A really good recent example that illustrates historical bias in the field of animal behavior and sheds light on the contributions of underrepresented minority pioneers and diversity activists is by Danielle Lee (2020). Over time with repeated examples, like these, perhaps students will begin to see these examples themselves when reading scientific literature, will think critically about assumptions that are made, and will begin to question the perspective from which scientific questions are even asked in the first place.

L.K.S.: In most of my classes, I have sessions in which we consider common misconceptions about behavior, evolution, and sex. These sessions often include considerations of how society influences science and vice versa, and how our scientific understanding of reproductive behavior has changed as a result of changes in society and the identities of the scientists. I also try to include an assortment of female-active and male-active examples.

Research and next steps

We highlight important steps researchers can take to improve the overall quality of our science. These include identifying the sex of subjects in our studies and challenging ourselves to question the how and why of our theoretical frameworks and methodology.

What major steps should researchers be taking?

Here we suggest a few ways that researchers may help improve the quality of science and reporting thereof.

V.H.: One thing researchers can do is to identify the sex of their subjects. Subject sex is routinely ignored and when included often the effect of sex is not assessed (Beery and Zucker 2011; Woitowich et al. 2020).

Even at the cellular level sex matters (Pollitzer 2013). For instance, skeletal-muscle cells from female mice regenerate faster than male cells (Deasy et al. 2007). How many researchers know or report the sex of the cells they use? Researchers using cells derived from the tumors of the African-American woman, Henrietta Lacks know the initial sex of HeLa cells. But the extensive aneuploidy in this line may make its current genetic sex uncertain (Adey et al. 2013).

At higher levels of biological organization, sex also matters and is not routinely reported. For instance, 68% (489) of the 722 posters presented at the 2020 SICB meeting did not report the sex of their study animals. Those 722 posters include 86 posters for which sex was not applicable (e.g., modeling, pedagogy, and botanical topics). If the "not-applicable" group is excluded, then 77% of the posters did not report subject sex. Why? If sex is important at the cellular level, then one would think it could be more important at higher organizational levels. As mentioned above, NIH now requires research they fund to include female subjects or explicitly state why such is not germane to the research. Perhaps the Society of Integrative and Comparative Biology could suggest that presenters always indicate the sex of their study subjects in all abstracts, posters, and talks as well as how sex was identified.

A.A.K.: To follow up on Virginia's comment—after identifying the sex of the subjects, it is so important to include sex in the statistical model as a fixed effect when the study includes both sexes. We look at females and males separately but determining sex differences can be better supported by a more vigorous statistical method.

N.L.S.: And not only report on the sexes examined, but include females in the study even if the traits are supposedly sexually dimorphic and not present in females. Traits that are defined as sexually dimorphic (in this case, in males only) in one species are assumed at times to be sexually dimorphic in other species, and then females are not included in the study, or the sample size is very low. There is a lot of natural variation out there in sexually dimorphic traits; we are biasing results if we do not study females as well. The degree of dimorphism itself is an interesting metric that varies.

T.J.O.: It is important not to rely on *argumentum ad antiquitatem* (appeal to common practice) in other words: "because we have always done x, y, z."

A.A.K.: Yes! I feel this really strongly in the argument of "it's easier to study males" in birds.

The argument is that males are easier to catch, sample, and observe. But really, it is not very costly to switch the focus to females. There are set "ways we do things" to catch and study males because there is a historical bias of studying males in the literature. That does not mean it will always be hard to study females if we put the effort into modifying our methods. Personally, I have actually been the most frustrated with data collection when studying females in the context that is the "preferred way" to study them—mate choice.

C.C.J.: In my first research experience, I was told that our work focused on males because "females introduced too many confounding variables." In the years since, I have come to realize that the false assumption that data on females is harder to collect and interpret is a direct result of biased research. Because of this historical bias toward males, even the methods we use may be skewed toward male physiology. As such, methods should be critically reassessed to ensure that they are most appropriate for the hypotheses we are testing.

As a physiologist, I have noticed that the dynamic nature of female reproduction is commonly overlooked when designing experiments. For example, many studies focus on comparing reproductive and nonreproductive females. While informative, this assumes female physiology during reproduction remains static throughout the course of the entire bout; "reproductive" is not a monolithic state. Accordingly, studies using reproductive females should include this temporal information when possible and experimental manipulations should aim to compare females who are at similar reproductive stages. Additionally, emphasis should be placed on understanding how physiology fluctuates over the course of a reproductive bout.

Dynamic changes also come in to play when interpreting results within the context of trade-offs. For example, recent interest has been placed on the role of oxidative damage in mediating costs of reproduction in females. In experiments comparing nonreproductive and reproductive individuals, samples are often taken while the individuals are still in a reproductive state, which is inherently inflammatory (Clancy 2013) and has been associated with increased oxidative damage (Yang et al. 2013). However, differences in oxidative damage measures may occur as a result of physiological changes necessary to support offspring production rather than as a cost of reproduction. Instead, Zhang and Hood (2016) suggest collecting tissues when females are no longer reproductive in order to parse out persistent costs of reproduction from transient changes.

K.A.H.: Start asking the hard questions, and find ways to work around the difficult-to-navigate female reproductive tract. Dig into researching technologies in other fields that might be useful for uncovering "cryptic" female processes so that we can get a better grasp on female biology. It is simply not enough to give up because it is hard to do. And when you are a reviewer, either for funding grants or publishingresearch articles, consider the concepts presented within this article and seek ways to support studies that account for the female perspective. Ask whether the female perspective was considered and what is missed if it wasn't.

C.C.J.: Tacking on to the point above: negative results are still results and should be reported. Negative results may provide valuable information about the degree of variation in a given trait (see above). For many physiological parameters, especially in nonmodel species, we do not have enough data to really get a sense of what a "normal" range of values is. This limits our ability to generalize our results and becomes problematic when trying to understand how your data stack up against data from other populations. Negative results can also contribute to a larger framework. For example, although the hypothesis that the large demands of reproduction necessarily incur costs to an individual's survival and/or future fecundity has predominated, supporting empirical evidence is scarce. In this example, negative results can inform us about the ubiquity of and the factors contributing to the costs of reproduction.

L.K.S.: Perhaps what I tell all of my students "be observant and open-minded to what you see." I think that we miss so much of what is going on in biology when we come in with a hypothesis before observing a system.

T.J.O.: Change may be difficult, but the payoffs include the advent of new sub disciplines, questions, and exciting conclusions. Cases such as symposia like this one, supported at SICB 2020, allow researchers to come together and discuss new ways forward and it is clearly evident that societies such as SICB are receptive to change.

So what should we be doing?

We can improve the quality of work that is being done such as by taking time to be meticulous in our language choice and being open to constructive discussion with other scientists.

V.H.: Minimally, the language we use needs to be carefully evaluated (examples in the introduction to this collection of papers).

M.F.W.: Preparing my talk for this symposium sensitized me to how terminology can include gendered terms that may inadvertently influence how one interprets results. For example, a male's seminal proteins have been said to improve a male's reproductive success by "manipulating" the mated female's physiology (or, for a less-loaded term, "influencing" or "regulating" it). If, instead, we look at the interaction from the female's perspective, perhaps she is using receipt of these proteins as a chemical signal that she has mated (and thus received sperm). This signal can then trigger her physiology to switch to favor progeny production. This new physiological state is energetically demanding, which would be disadvantageous until the female had received sperm needed for the gamete fusion to generate zygotes. Thus, rather than being manipulated by the male's seminal proteins, she is using them to actively control her own physiology. Reality is, in fact, a combination of both perspectives and, consistent with Teri's and Kristen's comments earlier in this article, also includes cooperation at the molecular level. In another example, the phenomenon known as "sperm competition" involves differential siring of progeny by the multiple mates of a single female. Although females play an active role in biasing which male's sperm are used ("cryptic female choice")—for example, sperm competition is not an all-male process despite its name—much of the literature is focused on those competing sperm, and how they can "win": more, faster, better sperm, and so on. Overall it is useful to pay attention to unintended implications of the terminology used in reproductive biology (see Table, Orr and Hayssen 2020 introduction, this volume). It can shape thinking without one being aware of this. When thinking about reproductive phenomena, it is useful to stop and consider them from the "perspective" of each sex.

T.J.O.: Key is to not throw the baby out with the bathwater; but to be sure we know that the bathwater is indeed bathwater and not something we mistook for bathwater. In other words, by being reflective of our research programs as well as of the terminology and assumptions we are using/making we can be more secure that what we have long-taken for fact is indeed true. In many cases, by leveraging these moments of pause, all researchers are challenging themselves to check for etymological, referential, or historical fallacies; to be certain that the use of a word as originally intended has not taken on a different meaning in today's society; and to realize that words in of themselves are not truth-bearing but aim to represent things; thus, the meaning of words stems in our use of them.

Another way to consider the female perspective is through the psychologist's fallacy (assuming one's own objectivity). Anthropologists are trained to question their own objectivity in research. Perhaps trainees in Organismal Biology would benefit for being challenged to do the same as they learn to conduct research.

D.J.S.: That is an excellent suggestion. When discussing this topic with other male colleagues I have been asked whether the "female perspective" on reproduction refers to the gender of the scientist or to the sex of the organism being studied. The latter interpretation is less disruptive to the *status quo* and therefore an easier sell, but there is a loss if we willfully ignore the perspectives we as researchers bring to the table. For a field such as reproductive biology to which our concepts of sex and gender are so intimately linked, achieving a completely objective, gender-neutral scientific approach would be difficult. Rather, we can recognize and embrace the partiality of different perspectives as ways to interact with the natural world (Haraway 1988). Incorporating reflexivity into our education would undoubtedly help build a socially responsible next generation of biologists, and a future where female and male scientists alike can continue to make insightful and meaningful contributions to reproductive biology. A distinction has been proposed between the detrimental partiality that is *bias* (which we can try to mitigate, e.g., by being mindful of language) and a productive form of partiality termed *valence* that comes from self-reflective exploration of alternative perspectives (Richardson 2013). Critical discourse between scientists taking diverse perspectives (Longino 1996) will help us collectively reach a greater understanding of reproductive biology. To those skeptical of the female perspective we present here as merely reversing the direction of bias or replacing an androcentric worldview with a gynocentric one, I believe this distinction is particularly relevant.

What progress is being made?

Here we remark on positives changes in the sciences around the study of females.

V.H.: NIH now requires that sex be addressed in clinical and preclinical research project. Editorial practices could follow suit. Although reviewers and editors may informally request that authors report sex in manuscripts this could be a formal requirement in their methods. Doing so will also make the data more useful for future comprehensive meta-analysis. In the author/presenter instructions, SICB could request inclusion of sex of subjects in abstracts, posters, or oral presentations.

For this issue, we created a "style sheet" for authors and copy-editors to use when writing or reviewing their text (appended to the introduction to these papers, Orr and Hayssen 2020). Similar devices could be more widely used to remind us of hidden assumptions or biases in our writing and publishing.

Spread the word; spur thinking. As an example, V.H. sent the Nature commentary "Cell Sex Matters" to colleagues who teach cell biology. The younger colleague said he would incorporate the study in his teaching. The older colleague knew of the work and proudly noted that the muscle cells he worked with were from female mice. V.H. asked if he reported the sex of his cells in his methods sections. He said, no, but that he would from then on. Also, in meeting with seminar speakers and job applicants and chatting with the presenters of posters, V.H. now initiates a conversion by asking about the sex of the person's research subjects; a much easier conversation to have one-on-one, than by asking the same question at the end of a colloquium!

K.H.: May I underscore the fundamental problem Teri notes, that words can take "on a different meaning in today's society; and . . . that words in of themselves are not truth-bearing but aim to represent things; thus, the meaning of words stems in our use of them." Negotiation about meaning goes on all the time, from all directions. It seems science would be impossible if we did not all use the same words in the same way. But we are multiple, with different experiences ourselves; and we are not the only ones using words. Policing the language seems cost paid for limited if any benefit. That view gives away my affiliation in anthropology where we continue to disagree about interpretations of the same observations. I certainly applaud raising questions about meanings and useful simplifications more often.

What terminology is biased or otherwise antiquated and promotes misguided conclusions? Alternatives and issues? EX: I often see scientists note "gender" instead of sex, perhaps something we can address?

We explore several terms that have been problematic historically.

A.K.L.: The literature contains numerous examples in which the terms "sex" and "gender" are conflated, treated as synonymous, and/or used inappropriately. Individual sex characteristics such as genital sex, gonadal sex, karyotypic sex, and so on, should be referred to as such. Sex cannot be assumed to be constant throughout a body or consistent with either karyotypic sex or with sex assigned based on genital sex. It is critical that biologists keep in mind that sex is not binary and that karyotypic sex need not align with other sex characteristics. The term "sex" refers to a category an individual is assigned at birth based on expected binary sex characteristics (typically based on external genitalia and/or karyotypic sex). Human sex is socially, societally, and culturally constructed based on assumptions of biology. "Gender" is socially, societally, and culturally constructed and is a performance of masculinity and femininity. Nonhuman animals, plants, and fungus do not have gender.

As biologists, we use terms in our research and teaching that have complicated and varied definitions. These terms are also used outside of our academic disciplines, complicating their uses, as science communication and translation for those outside academic science are prioritized. Queer theorist Judith Butler (2005, 21) reminds us that language constantly evolves and no term exists in a vacuum:

> The very terms by which we give an account, by which we make ourselves intelligible to ourselves and to others, are not of our making. They are social in character, and they establish social norms, a domain of unfreedom and substitutability within which our "singular" stories are told.

Biologists frequently use the terms "feminine" and "masculine," as well as their derivatives "feminize," "feminized," "feminization," "masculinize," and so on. in order to describe sex characteristics. "Feminine," "masculine," and their derivatives are associated with gender in everyday language, rendering the usage of these gendered terms in sex biology problematic. Academic science does not exist in a vacuum, and constant cross-talk between academic science and society can inadvertently superimpose gender onto sex. While it is generally understood that gender is not binary but is rather a spectrum, and so on, and that sex characteristics are not binary either, the terms "masculinize" and "feminize" do not accurately represent the spectral nature of sex characteristics. Biological characteristics and their various states can and should be described without employing this gendered language.

V.H.: According to NIH "Sex is a biological variable defined by characteristics encoded in DNA, such as reproductive organs and other physiological and functional characteristics. Gender refers to social, cultural, and psychological traits linked to human males and females through social context. In most cases, the term 'sex' should be used when referring to animals" (NIH Guide Notice 2015).

L.K.S.: In the field of evolution of behavior, some terms that concern me are the use of "strategic" for changes in sperm allocation and "differential" for changes in egg allocation. Another one that I find problematic is "convenience polyandry" which is the idea that females mate with multiple males in order to avoid the costs of male harassment. There are problems with this term both scientifically in how to test the hypothesis (Boulton et al. 2018) and culturally in the implication that mating to avoid harassment is in any way "convenient."

What are some issues with terminology?

We comment on the following remark by a symposium attendee: I think a lot about when to use the words "egg," "ovum," "embryo," and other related terms, since "egg" is used in so many ways. I agree that some consider the term "fertilization" is problematic, but I think it is harder to substitute "conception" when gamete fusion is external.

V.H.: I agree but with time perhaps the wording would not feel so odd. In some cases, syngamy or gamete fusion may also be alternatives to "fertilization." A textual example: When gamete fusion is external, environmental factors have a large influence on the process, the dynamics, and the eventual success of the fusion. No gamete "choice" occurs, and random mixing of maternal and paternal genomes may be predominant (although that is an untested assumption on my part). With external gamete fusion neither sex is "active" or "in control." When gamete fusion is internal, usually within a female's body, then the female has great control over when this fusion occurs, where it occurs, and with which paternal genome is used.

A.A.K.: I would like to note that switching away from egg makes sense in the mammal context, and when discussing the ovum when it is still internal; but the word "egg" has another context for egg-laying species (birds and reptiles) in which it describes an ovum that has been shelled and serves as a place for the embryo to grow outside of the body.

V.H.: You make a good point that also applies to mammals since monotremes also lay "eggs" that is shelled embryos. The hard shell is a vertebrate "invention" leading to the cleidoic "egg."

Ova and developing embryos are distinctly different in an evolutionary and reproductive context, but the word "egg" is sometimes used for both. For instance reproduction in viviparous lamniform sharks includes both oophagy and siblicide, but the paternal genome could be involved in the latter (siblicide) but not the former (oophagy).

We need terminology that distinguishes between ova and the various products of ova development with or without conception. The presence of extensive yolk, the presence of syngamy (i.e., the combination of the two parental genomes), the presence of a hard shell are all distinct traits that are subsumed indiscriminately by the word "egg." I just do not know what terms to substitute.

K.E.H.: I believe we need to include some caveats about choice of language here so that the changes we are suggesting are taken seriously by readers. Let me give you a real-life example. I run a long-term study of spotted hyenas in Kenya. Each year I send several undergraduate students to spend a year abroad, working as Research Assistants on my project. A couple years ago, when pronoun identification became more prevalent, observation sessions started showing up in our field notes that referred to a single hyena as "they." Not only does this fail to enhance clarity, but I also spent many extra hours searching for the other hyenas in field notes wherever a single hyena was referred to as "they." In science it seems to me that we do not want to sacrifice precision in our language for the sake of political correctness.

Conclusion

Within this article, we have asked questions about reproductive biology through a female lens that we hope the reader will consider for themselves in any and all of their professional roles as researchers, mentors, teachers, editors, and reviewers. We also hope that the contributed manuscripts within this edition of ICB will serve as a paradigm shift for advancing our understanding of female reproduction. We hope for a change similar to the paradigm shift in evolutionary biology precipitated by Gould and Lewontin (1979) when they questioned the assumption of adaptation by natural selection as the sole explanatory framework for evolution. We believe our understanding of reproductive biology is similarly limited when a male-centric framework is the first, and sometimes only, approach to research. By considering the female perspective, we can shed light on the diversity, mechanisms, dynamics, and consequences of the substantive investment females make in reproduction. We believe this additional perspective provides an exciting future research direction within the field as it has in other scientific fields (Criado-Perez 2019).

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