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SYMPOSIUM

Misconceptions about Conception and Other Fallacies: Historical Bias in Reproductive Biology

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Synopsis Natural selection (differential reproduction) is a major tenet of evolutionary theory. In mammals the success of reproduction is primarily controlled by females who provide the majority of offspring care via gestation and lactation. In some species, maternal care also extends post-weaning. This primacy of female reproduction in evolution has not quite crept into our understanding of organismal adaptations in anatomy, physiology, and behavior. This cultural legacy has left its mark and led to misconceptions in our understanding of reproductive biology that are especially prominent in the understanding of reproduction in the general public. Here, I give examples of such misconceptions. I focus on aspects of physiology (the "sperm race," the "estrous cycle," the "28-day" menstrual cycle, "sex" hormones, and meiosis) as well as aspects of terminology in morphology and behavior. The issues I raise are not new, but all remain embedded in the teaching of reproductive biology especially at the introductory level. For each issue, I examine the historical bias, the consequences of that bias, and, more importantly, ways to ameliorate that bias going forward.

Introduction

Culture influences science. The processes of discovery and understanding, of naming and theorizing, are strongly influenced by the values and gestalt of the individual scientists doing the work. This is not a new concept. As Blackwell noted in 1875 "The older physiologists not only studied nature from the male standpoint—as, indeed, they must chiefly, being generally men—but they interpreted facts by the accepted theory that the male is the representative type of the species—the female a modification preordained in the interest of reproduction, and in that interest only or chiefly." As a current example from animal behavior, look at polar bears. Although polar bears are considered solitary, female polar bears live nearly all their lives in the company of their offspring. Females have constant social interactions with their cubs and they interact with their environment as part of a social group, not as solitary individuals. How they hunt, how far they roam, how they thermoregulate, how much they are exposed to pathogens, how much they need to scan the environment for predators, all these aspects of their lives differ from those of a solitary individual. So, why then are polar bears usually considered solitary? The perception of polar bears as solitary is likely because this is a characteristic of male polar bears, and male behaviors are often chosen to represent the species behavior. Males are generally solitary; females generally are not. Why do we devalue the importance of reproduction in our assessment of the biology and ecology of animals?

The answers chiefly lie in the cultural attitudes, assumptions, and language of the individuals who did the science. In reproductive biology, these individuals were predominately white, western men, e.g., Aristotle (384–322 BCE), Gabriele Falloppio (1523–1562), or Regnier de Graaf (1641–1673). Thus, the historical bias in reproductive biology is grounded in who did the science. That bias is sustained through cultural acquiescence and culturally-laden language and leads to misconceptions about how reproductive processes work (Schatten and Schatten 1983; Beldecos et al. 1988; Martin 1991). The bias continues today (Beery 2018; Mamlouk et al. 2020).

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Here I will briefly review entrenched aspects of reproductive biology that perpetuate inaccurate understandings of reproductive physiology. While reproductive scientists at large often understand the inaccuracies, textbooks and the popular press continue to mislead students and thus the larger community. The concepts I will address are the "sperm race," the "estrous cycle," the "28-day menstrual cycle," sex hormones, and meiosis. Terminology can maintain or reinforce androcentric bias. Consequently, I also discuss terminology for various aspects of reproductive anatomy and behavior that show evidence of historical bias. In at least one case, gender-biased terminology may have consequences for medical diagnosis.

The "sperm race": misconceptions about conception

The scientific community has known for over 70 years that "it is highly unlikely that sperm motility has the slightest value for ascent through the oviduct" (Hartman 1957, 419). Yet, even in 2016, Holt and Fazeli (2016) needed to repeat that "the 'sperm race' is no longer a tenable hypothesis" (105). The inaccuracies of this metaphor have been discussed repeatedly (e.g., Schatten and Schatten 1983; Beldecos et al. 1988; Martin 1991), yet it persists. The concept is so firmly entrenched that even a 21st century paper on oviductal fluid-dynamics makes sperm the titular active agents (Ishikawa et al. 2016). This female-passive, male-active stereotype began with Aristotle who believed a sperm provides the essence and soul of humanity (which is a replication of manhood) and a female's ovum passively provides the material from which to create the body (Freeland 1987).

The "ovum passive, sperm-active" generalization permeates the scientific literature in reproductive biology. Three aspects of the popular understanding of conception are misleading or inaccurate: the sperm "race" itself, sperm competency, and ovum "passivity." The "sperm race," as popularly used, primarily applies to mammals. As such, this discussion will revolve around mammalian conception but the female-passive, male-active stereotype is reflected in other aspects of reproductive biology, such as sexual behavior.

First, sperm do not race to the site of conception. In fact, sperm in some taxa are aflagellate and nonmotile (Morrow 2004). Notwithstanding the presence of flagella and mitochondria, mammalian sperm do not have the energetic resources or directional ability to travel under their own power to the site of conception (Hartman 1957). In fact, the female tract is dynamic and active, not static and passive. The female tract regulates the movement of sperm.

The vagina, uterus, and oviducts are not a solid, immobile, mountain range, as portrayed in a 2010 National Geographic documentary (no longer available), but an undulating and anatomically complex, fluid-filled system with furrows and ridges, reservoirs and pouches, cilia and muscle (Suarez 2016). The uterine and oviductal fluid "is rarely static: ciliary beating, contractions of smooth muscle," and secretions of additional fluid direct the movement of gametes as well as potential pathogens (Suarez 2016, 186). The fluid's viscoelastic properties modify the bending and trajectories of sperm (Suarez 2016). Orgasmic and other contractions alter the fluid dynamics of the female reproductive tract and propel or impede sperm as appropriate (Holt and Fazeli 2016). Portions of the tract will store sperm for later use (Suarez 2016). At the junction between the vagina and the uterus, microgrooves in the cervix serve to place sperm in the proper orientation to enter the uterus (Suarez 2016). A second junction, between the uterus and the oviducts, is highly variable both across species and across reproductive states (Suarez 2016). This junction is a key place where the female tract selects which sperm will be released into the oviducts (Pérez-Cerezales et al. 2018). Conception occurs in the upper reaches of the oviducts. Thus, the movement of sperm from the site of deposition to the site of conception is regulated by the female reproductive tract.

Second, when mammalian sperm are deposited in the female reproductive tract they are incompetent. That is to say, they are biochemically, physiologically, and physically not able to fuse with an oocyte even if they could "race" to it (Pérez-Cerezales et al. 2018). In fact, sperm must undergo "physiological preparation within the female reproductive tract before they are capable" of fusing with an ovum (Austin and Bishop 1958, 851). This multi-step process is termed capacitation and is regulated by the female's reproductive tract. For humans, capacitation begins in the cervical mucus of a periovulatory female where sperm "are scrubbed by the ultrastructural elements in the mucus" (De Jong 2017, 291). In this way, the cervical mucus, itself, selectively traps or inhibits sperm. Additionally, leukocytes within the mucus produce molecules that have a "deleterious influence on dysfunctional sperm" and a positive influence on other sperm (De Jong 2017, 291). Thus, before sperm are released to the uterine lumen, and eventually to the oviducts, the female's physiology has begun filtering the original cohort.

The selection of sperm continues in the uterus and oviducts. As "uterine contractions ... propel sperm" through the uterus, uterine secretions alter the plasma membrane of sperm so it becomes regionalized with altered ionic permeability and receptor expression (De Jong 2017, 291). In addition, the uterine lumen greatly alters the metabolism of sperm (Chang 1957). The oviduct and its fluid are also involved in the capacitation of sperm. Not only is the oviduct the site of conception, with key roles in the early development of the embryo, but it is also another location where sperm are selected, stored, and biochemically altered so that they are able to receive cues from the oocyte and its cloud of ovarian cells (Pérez-Cerezales et al. 2018). In fact, the oocyte and surrounding cumulus cells secrete molecules that bring sperm toward them (De Jong 2017). Thus, the filtering of sperm occurs continuously from the site of deposition to the location of the ovulated oocyte.

The selective ability of the female tract is significant. In fact, "in all mammalian species examined to date ... of the many millions of spermatozoa ejaculated, only tens to hundreds reach" the site of conception (Zukerman et al. 1977; Pérez-Cerezales et al. 2018, 265). Even at the oocyte, the ovarian cells surrounding the oocyte and the zona pellucida (an acellular layer around the oocyte) modify sperm to enable conception. This brings us to the third point.

Third, engulf or penetrate? Does an ovum engulf a sperm or does a sperm penetrate the ovum? Of course, neither metaphor is accurate but the "penetration" metaphor has colloquial dominance. When an oocyte and sperm first contact one another, tiny microvilli, populating the surface of the oocyte, elongate into "extremely fine, fingerlike projections that clasp the sperm head and eventually entwine even its tail" (Schatten and Schatten 1983, 32). Even before contact, the ovarian cells (the cumulus) that accompany the oocyte during and after ovulation control "the access of spermatozoa to the oocyte" (Tanghe et al. 2002, 414). These ovarian cells function to attract, trap, and select sperm as well as chemically alter sperm to facilitate conception (Tanghe et al. 2002). Listing the actions the oocyte takes in order for conception (syngamy) to occur may influence how we view the dynamic between oocyte and sperm. The oocyte digests the sperm head, degrades the tail, encases the sperm DNA to form a pronucleus, encases ovum DNA to form a pronucleus, degrades paternal mitochondria, builds the machinery needed to pull the pronuclei together, and thus creates a single nucleus. All the material for this activity comes from maternal resources that are deposited in the ovum before conception. Sperm contribute little to the success of this process. In fact, even at the surface of the oocyte (the zona), "the flagellum produces forces on the [sperm] head which act in directions tending to pull the sperm away from the zona during much of each flagellar beat" (Baltz et al. 1988). Relative to oocytes, sperm do little to facilitate conception.

In sum, sperm do not race to the site of conception. Muscular contractions and ciliary action alter the fluid dynamics of the female tract, moving sperm in one direction toward the site of conception and ova from the ovary in the opposite direction. Female secretions biochemically alter sperm to make conception possible. In general, once a female obtains sperm, her resources manage their action and function as well as conception itself. Thus, in contrast to the general view, conception is a female-active, male-passive process. We need to recognize that fact going forward and a small step would be to use the gender-neutral term "conception," rather than the female-passive, male-active term "fertilization." More importantly, we need to recognize, not only in our teaching at the introductory level, but also in our writing, the simplistic fallacy of the "sperm race" and concentrate instead on the complexity of interactions that result in the creation of an embryo.

The estrous "cycle" is an artifact of captivity

While misconceptions about conception as a "sperm race" are predominantly an issue with understanding human physiology, more relevant to mammals in general is the cultural assumption that female mammals have repeated, non-pregnant cycles, in other words, the concept of a regular estrous cycle. However, "[i]n natural populations the nonpregnant cycle is a rarity, and it is essentially a pathological luxury which cannot be tolerated" (Conaway 1971, 239). In fact, the usual reproductive cycle for mammals is as follows: ovulate, conceive, gestate, release uterine progeny, lactate, and repeat. For seasonal species (either for cold or drought), lactation may be followed by a non-reproductive period before folliculogenesis resumes. Thus, the entire concept of an estrous cycle is a human construct and, for domesticated species or zoo animals, an artifact of captivity. In captive and laboratory animals, hormones are easy to measure, repeatedly, over time, but these endocrine variations do not represent the natural hormonal profiles of reproductive females in the wild. Like basal metabolic rate (BMR), "cycle" length is a

useful measurement tool but not a natural phenomenon.

The artificial construct of an estrous or menstrual "cycle", which had predictable hormone levels at predictable times, is an artifact of our ability measure these levels and our ability to compute means and standard errors from them. These numbers suggest regularity where none exists. Instead variability is probably more significant in natural situations, even for humans.

The menstrual "cycle" is not 28 days

Menstrual cycles provide two examples of cultural bias and both examples have consequences. First, the "28-day cycle." The length of the human menstrual cycle is popularly considered to be 28 days. It is not. In 1939, Leslie Arey analyzed 17,652 cycles from 1265, mostly western, women aged 17–49 years. For both adolescent and adult women, neither the mode nor the mean cycle length was 28 days. Adolescent (young adult) women had modal cycles of 30–31 days (mean 33.6 days; range 1–69 days) whereas cycles for adult women were shorter with a mode of 27 days (mean 29.5 days; range 6–211 days). In fact, many women rarely had an individual cycle that matched their own average cycle length. For adolescent cycles, one-third of 100 women, in their first 31 cycles never had a cycle that corresponded with their own mean cycle-length. Similarly, in a given year, 27% of >500 women never had a cycle that corresponded with their own mean cycle-length. In short, women do not have cycles at 28 days (lunar) intervals. Variation in cycle length is the norm. To say that one's period is early or late (with the associated angst) is to buy into the misleading cultural notion that cycle length is highly regular. It is not. Variability is normal, not regularity.

Second, the belief in a standardized hormonal cycle has medical consequences, especially for infertility research. For instance, the medical concept of a "luteal deficit" arises when a women has less than a 14-day luteal (high progesterone) phase (the interval between ovulation and menstruation). In fact, short luteal phases with lower progesterone levels are common in fertile women (Clancy et al. 2009). Clancy and her colleagues compared rural, Polish women to urban US women of similar age (mean: 28.6–29.1 years, range: 20–40 years). The Polish women had lower progesterone levels as well as a shorter luteal phase, but these differences did not lower fertility. In fact, lower hormone levels were associated with higher fertility, as 73% of the rural women had children compared with none from the urban sample (Clancy et al. 2009). These results challenge the medical practice in fertility regimes, which is to administer hormones at higher than physiological levels (Clancy et al. 2009). Tangentially, in other species, high progesterone can occur before ovulation, as in cows, or before and after ovulation, as in giraffes (Hayssen and Orr 2017). Thus, the human hormonal profile does not extend to other species. More importantly, lack of a 14-day luteal phase should not be the basis for medical intervention.

Estrogens and androgens are not sex-specific

As Elizabeth Adkins-Regan noted, "the association of androgens with masculine traits and estrogens with feminine traits is also a poor fit with nature's ways" (Adkins-Regan 2005, 6). Hidden assumptions, based on terminology, can bias research. The word "androgen" comes from the Greek "andro" for "a male human," whereas "estrogen" is from the Greek "oestrus" meaning "frenzy" or "gadfly." If androgens such as testosterone are identified as "male" hormones with links to "male" qualities (e.g., aggression) then other behavioral effects (e.g., cuddling or reactions to crying babies) may not be examined (van Anders et al. 2011). In fact, testosterone is positively correlated both with partner cuddling and responses to crying babies (Bos et al. 2010; van Anders et al. 2011). The round-table discussion paper at the end of these symposium papers provides more details on problems associating estrogens with "female" and androgens with "male" traits (Orr et al. 2020, this volume).

Meiosis is not just spermatogenesis, but you would not know that from textbook depictions

Meiosis is the well-known process of cell division that generates haploid gametes from diploid stem-cells. The process generates both female gametes (oogenesis) and male gametes (spermatogenesis), but textbook diagrams only illustrate male meiosis (Gorelick 2012). You can use a google-image search for meiosis and see for yourself. Doing so results in many, many rows of isogamic meiosis (i.e., spermatogenesis) and almost none for anisogamic meiosis (i.e., oogenesis). Even images recovered from a search for "female meiosis" or "oogenesis" often also include spermatogenesis, but images recovered for "spermatogenesis" rarely include oogenesis. This kind of gender bias is hidden but pervasive. Less

hidden are the names given to female anatomy and behavior.

Terminology in reproductive biology

The names given to parts of female anatomy are of concern to feminists, although some of the bias associated with some terminology is so far in the past as to be invisible. For instance, the etymology of "vagina" is from Latin for "sheath" or "scabbard" and clearly not from the female perspective. That viewpoint of the vagina may have had influence on reproductive science long ago, but currently very few people are even aware of the androcentric bias. However, the names of other parts of female bodies have not escaped current notice. "The truth is, men are all over women's bodies—dead, white male anatomists, that is. Their names live on eponymously, immortalized like audacious explorers for conquering the geography of the female pelvis as if it were terra nullius" (Kaminsky 2018). In fact many parts of female anatomy, from Graafian follicles and Fallopian tubes to the G-spot, have been named after men, but no male body parts are named after women. Does it matter? Some feminists argue it does. Using male-centered words for female anatomy focuses on the "historical victories of men 'discovering' body parts" (Kaminsky 2018). The subliminal message is that female body parts are objects that are important for the male who "discovered" them and not for their reproductive function (Kaminsky 2018). But their reproductive function is the thing that matters to scientists and since we have alternative names that focus on function rather than discovery (see Orr and Hayssen 2020, Table 1, this volume) perhaps we should use those. More important is the fact that female anatomy is studied in far less detail than that of males.

Anatomical terminology has an androcentric bias with fewer terms for female anatomy

The *Terminologia Anatomica* is the international standard for human anatomical terminology with names for ~7500 macroscopic anatomical structures. Developed by the Federative Committee on Anatomical Terminology and the International Federation of Associations of Anatomists, the index provides anatomical names for structures in all anatomical systems including female and male genitalia. We can use the number of named structures as a proxy for the amount of detailed study for each sex. If no bias exists the number of names for each sex should be equal, but they are not.

In the *Terminologia Anatomica* female anatomy has fewer named features. Under "genital systems," the "female" section lists 130 terms while the "male" section lists over 15% more (151 terms). This may simply indicate that female anatomy is less complex than male anatomy, but further exploration points to a different conclusion.

Similar structures are found in both females and males. The gonads are an example. The ovary has 18 terms listed whereas the testis has 25. Both sexes have a urethra: that for females has 16 terms (excluding the prostate), while 32 terms are named for the urethra in males. Both sexes have a prostate gland. For males the structure is given 23 terms while the gland is not even named as such for females but combined with the urethra. Even with identical structures, scientists labeled fewer details in female anatomy than in male anatomy.

What causes these discrepancies? The answer may be a consequence of who did the naming and the cultural attitudes surrounding sex and gender. The terms describing the penis reflect a markedly more detail-oriented approach than that taken when examining the clitoris. Clitoral anatomy is a prime example of historic androcentric-bias in biological science. In a detailed review O'Connell and her colleagues (2005) document that for centuries the clitoris was historically ignored or treated as an abnormality by anatomists. Even textbook "descriptions of the clitoris lack detail and include inaccuracies" (O'Connell et al. 2005, 1189). When textbooks are inaccurate then future generations of medical practitioners and scientists will continue those errors. More importantly, sometimes this mis-naming has medical consequences.

Prostate: females have one

A few words about the prostate: a case where the mis-naming has medical consequences. With the prostate, Aristotle has a bit of a reprieve. He noticed that "the discharge accompanying sexual pleasure in the female contributes nothing to the embryo"—"the actual discharge does not take place within the uterus ... but it is in the region in front of this, where the female discharges the moisture ... [where] the male emits the semen" (Smith and Ross 1912, 738–9). Women (and other female mammals) have a prostate gland (Hayssen and Orr 2017). It is in the same position as in males, secretes the same secretions, and also expresses prostate-specific antigen (PSA; Pollen and Dreilinger 1984; Tepper et al. 1984; Biancardi et al. 2017). It has the same embryology; the same

biochemistry, structure, and vasculature; and produces an ejaculate (squirting) (Zaviačič 1999; Zaviačič and Albin 2000; Zaviačič et al. 2000). It can also become cancerous (Tsutsumi et al. 2018) with 1615 cases in women in the USA from 1973 to 2002 (Delli'Atti and Galosi 2018). In fact, adenocarcinomas of this gland "recapitulate morphologies and immunohistochemical markers seen in prostatic adenocarcinoma" (Tregano and Epstein 2018, 1513) and can metastasize (Sloboda et al. 1998). In addition, the usual treatments for prostate cancer can be effective (Korytko et al. 2012); that is, assuming the diagnostician knows to look for a prostate in her or his female patient in the first place. Unfortunately, use of the term "Skene's gland," instead of "prostate," "incorrectly implies that some structure other than the prostate" may be involved in a cancerous condition (Zaviačič and Ablin 2000, 131). This mis-naming could potentially delay diagnosis and treatment. Thus, bias in the naming of structures can have significant consequences.

Penis: not just for males?

But let's examine some more obvious anatomical structures. For example, what is a penis? For you, does the term refer to morphology, embryology, function, or something else? Female spotted hyenas (*Crocuta crocuta*) have large genitalia. In fact, the external morphology of female and male genitalia is nearly identical (Hamilton et al. 1986). Functionally, they differ. The spotted hyena clitoris is used not only for urination and mating, but also for birth. Is this structure a penis (which is exactly what it looks like), a pseudo penis, a female phallus, or an enlarged clitoris. If we define a penis as a structure for transferring sperm from males to females, then enlarged clitoris is my personal preference. However, another female has a reproductive structure that stretches the envelope even further.

A tiny (2–3 mm) Brazilian cave insect, *Neotrogla*, subsists on scavenging bat carcasses and bat guano. More notably it has copulations that last 40–70 h. Even more notably, the female "deeply penetrates the male" (Yoshizawa et al. 2014, 1006). She inflates her penis within the male and numerous spines on her penis anchor her to him. During the long copulation, she absorbs/imbibes his spermatophore (sperm plus nutrients) (Yoshizawa et al. 2014). The authors might well argue that their discovery has made millions of dictionaries outdated, if those dictionaries define a penis as a "male genital organ" as many do. One might call the structure an intromittent organ, but that term is defined as a structure that enters the female genital tract and deposits sperm (Kelly and Moore 2016) rather than entering the male and retrieving sperm. However, if a penis is an organ that moves sperm between females and males, then females of this Brazilian insect have a penis. So defining a penis is challenging; what about defining an egg?

Ovum, blastocyst, zygote, or conceptus, but not egg

"In laboratory parlance, and even in print, the oocyte ... ovum, zygote, morula and blastocyst are frequently referred to indiscriminately as the 'egg'" (Perry 1981, 321). In using the word "egg," we conflate the female gamete (an oocyte or ovum) with the product of conception (a zygote). The term "egg" is used so imprecisely in common language that it has lost the ability to coherently describe reproductive cells in all of their states. Look at three uses of the word "egg." First, the term "egg" is used to describe a female gamete (an oocyte or ovum); a large cell with the maternal nuclear and mitochondrial genome as well as an extensive cytoplasm. Second, an "egg" is a zygote (blastocyst, conceptus) that contains both maternal and paternal genes. The use of "fertilized egg" only reinforces the female passive-male active misunderstanding of conception. Lastly, an "egg" is understood as something we eat for breakfast, technically this is a cleidoic, or shelled, "egg." Female gametes and zygotes are not equivalent. To use the same word for both compromises our understanding of each.

Conception, gamete fusion, or syngamy, but not fertilization

The terms insemination, fertilization, and impregnation are all female passive–male active, whereas "conception," "gamete fusion," or "syngamy" are gender neutral. However, to establish their regular use, we need to be comfortable with gender-neutral phrases such as internal conception, external syngamy, delayed gamete fusion, or artificial conception. These phrases seem awkward because they are not familiar. More problematic is the verb "fertilize" for which we have no neutral alternative. Conceive and fertilize should be opposites, but culturally they are not. For instance, to conceive of an idea is not the same as to fertilize it. Language is highly nuanced. Problems with the names given to female sexual behavior are less nuanced.

Female sexual behavior: solicitation not attractivity; facilitation not receptivity

The study of female sexual-behavior is an example of using a male framework to assess a female behavior. Since most research into sexual behavior was done by men, the measurement of female behavior is often in terms of male response. A highly regarded textbook in behavioral neuroendocrinology (Nelson 2011) provides an example of how the male lens is still used to define female traits. In the textbook, two components of female sexual-behavior are defined in terms of males: first, "attractivity": "the stimulus value of a female to a male" and second, "receptivity": "the stimulus value of a female for eliciting an intravaginal ejaculation" (Nelson 2011, 289). The text relies on an almost 45-year-old assessment of female sexual-behavior (Beach 1976). Beach formulated his operational definitions in the framework of simple stimulus–response interactions. Although Beach (1976) acknowledged the equal contribution of both females and males to conception, he created operational definitions of "feminine sexuality" (105) that focused on the "observation of behavior of conspecific males toward the female" because, for him, male behaviors were "susceptible to quantitative measurement" (106). Beach (1976) acknowledged the heuristic simplicity of his model. In fact, for Beach's (1976) definitions to accurately reflect variations in female behavior, all the males used to assess female behavior would have to be in identical hormonal states, have equal sensory abilities, be of equal readiness, and have the same reproductive histories. If not, then the measures could be assessing a male's ability to be attracted rather than female "attractivity" or "receptivity." These difficulties with the assessment tool were not discussed by Beach or by Nelson.

Of course, female behavior could be measured from the female's point-of-view. For instance, instead of defining "attractivity" we could assess an equivalent concept such as "solicitation" and explore variability in the behaviors and cues females use to find potential mates. Or instead of assessing "receptivity" in terms of male ejaculation we could assess "facilitation" and document the behaviors and cues females use to achieve conception, which would, of course, include female movements, vocalizations, and pheromonal release before, during, and after coitus. The multi-modal "clitoral winking" (Asa 1986, 521) in mares is an excellent example of the complexity of behaviors females use to achieve conception (Asa 1986).

Proceptivity, a third term used for female sexual-behavior (Beach 1976), also has a male bias. Sex drive, or libido, is often assumed to be equivalent to proceptivity, but as Hrdy (2000, 80) noted, comparing the "sex drive" of a potentially fertile male with a non-ovulating female, or "[assuming] that the urge to mate derives from the same "motivation" or evolved for the same reason in both sexes" is the biological equivalent of comparing apples to oranges (Hayssen and Orr 2017). Comparing the libido of an estrous mare with that of a gelding would be an equivalently mismatched juxtaposition. Both females and males have heightened libido when mating is hormonally advantageous. Females have more obvious hormonal peaks and troughs with resultant behavioral changes. Males are under more consistent hormone levels (albeit with often-ignored fluctuations). Overall, defining sexual behavior from the male perspective suggests that females are not soliciting mating nor actively participating in the process.

Concluding remarks

The specific androcentric biases in reproductive biology that I raise in this paper are only a subset of the intersection of culture and the study of reproduction in humans and other taxa (including plants, protists, fungi, and bacteria). None of the issues is new (Blackwell 1875; Beldecos et al. 1988), but all remain embedded in the teaching of reproductive biology especially at the introductory level. We can move to ameliorate the influences of our cultural history on our science. Language is one key. The introduction to this set of papers includes a table of gender-neutral terms to use instead of the generally-androcentric, historical ones (Orr and Hayssen 2020). Awareness of and conversation about bias is also key. As writers, reviewers, editors, scientists, professors, and citizens, we have venues for changing the ways in which reproductive biology is framed. We should use them. We are all in this together.

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References

Austin CR, Bishop MWH. 1958. Capacitation of mammalian spermatozoa. Nature 181:851.

Adkins-Regan E. 2005. Hormones and animal social behavior. Princeton (NJ): Princeton University Press.

Arey LB. 1939. The degree of normal menstrual irregularity. An analysis of 20,000 calendar records from 1,500 individuals. Am J Obstet Gynecol 37:12–29.

Asa CA. 1986. Sexual behavior of mares. Vet Clin N Am Equine 2:519–34.

Baltz JM, Katz DF, Cone RA. 1988. Mechanics of sperm-egg interaction at the *zona pellucida*. Biophys J 54:643–54.

Beach FA. 1976. Sexual attractivity, proceptivity, and receptivity in female mammals. Horm Behav 7:105–38.

Beery AK. 2018. Inclusion of females does not increase variability in rodent research studies. Curr Opin Behav Sci 23:143–9.

Beldecos A, Bailey S, Gilbert S, Hicks K, Kenschaft L, Niemczyk N, Rosenberg R, Schaertel S, Wedel A the Biology and Gender Study Group. 1988. The importance of feminist critique for contemporary cell biology. Hypatia 3:61–76.

Biancardi MF, Dos Santos FCA, de Carvalho HF, Sanches BDA, Taboga SR. 2017. Female prostate: historical, developmental, and morphological perspectives. Cell Biol Int 41:1174–83.

Blackwell AB. 1875. The sexes throughout nature. New York (NY): G.P. Putnam's Sons.

Bos PA, Hermans EJ, Montoya ER, Ramsey NF, van Honk J. 2010. Testosterone administration modulates neural responses to crying infants in young females. Psychoneuroendocrinology 35:114–21.

Chang MC. 1957. A detrimental effect of seminal plasma on the fertilizing capacity of sperm. Nature 179:258–9.

Clancy KBH, Ellison PT, Jasienska G, Bribiescas RG. 2009. Endometrial thickness is not independent of luteal phase day in a rural Polish population. Anthropol Sci 117:157–63.

Conaway CH. 1971. Ecological adaptation and mammalian reproduction. Biol Reprod 4:239–47.

De Jong C. 2017. Biological basis for human capacitation—revisited. Hum Reprod Update 23:289–99.

Dell'Atti L, Galosi AB. 2018. Female urethra adenocarcinoma. Clin Genitourin Cancer 16:e263–7.

Freeland C. 1987. Aristotle on bodies, matter, and potentiality. In: Gotthelf A, Lennox JG, editors. Philosophical issues in Aristotle's biology. Cambridge: Cambridge University Press. p. 392–407.

Gorelick R. 2012. Meiosis is not gender neutral. BioScience 62:623–4.

Hamilton WJ III, Tilson RL, Frank LG. 1986. Sexual monomorphism in spotted hyenas, Crocuta crocuta. Ethology 71:63–73.

Hartman CG. 1957. How do sperms get into the uterus? Fertil Steril 8:403–27.

Hayssen V, Orr TJ. 2017. Reproduction in mammals: the female perspective. Baltimore (MD): Johns Hopkins University Press.

Holt WV, Fazeli A. 2016. Sperm selection in the female reproductive tract. Theriogenology 85:105–12.

Hrdy SB. 2000. The optimal number of fathers. Ann N Y Acad Sci 907:75–96.

Ishikawa Y, Usui T, Yamashita M, Kanemori Y, Baba T. 2016. Surfing and swimming of ejaculated sperm in the mouse oviduct. Biol Reprod 94:1–9.

Kaminsky L. 2018. The case for renaming women's body parts [online]. BBC.com (https://www.bbc.com/future/article/20180531-how-womens-body-parts-have-been-named-after-men).

Kelly DA, Moore BC. 2016. The morphological diversity of intromittent organs. Int Comp Biol 56:630–4.

Korytko TP, Lowe GJ, Jimenez RE, Pohar KS, Martin DD. 2012. Prostate-specific antigen response after definitive radiotherapy for Skene's gland adenocarcinoma resembling prostate adenocarcinoma. Urol Oncol Semin Ori Invest 30:602–6.

Mamlouk GM, Dorris DM, Barrett LR, Meitzen J. 2020. Sex bias and omission in neuroscience research is influenced by research model and journal, but not reported NIH funding. Front Neuroendocrinol 57:100835 (https://doi.org/10.1016/j.yfrne.2020.100835).

Martin E. 1991. The egg and the sperm: how science has constructed a romance based on stereotypical male–female roles. Signs 16:485–501.

Morrow EH. 2004. How the sperm lost its tail: the evolution of aflagellate sperm. Biol Rev 79:795–814.

Nelson RJ. 2011. An introduction to behavioral endocrinology. 4th edn. Sunderland (MA): Sinauer Associates, Inc.

O'Connell HE, Sanjeevan KV, Hutson JM. 2005. Anatomy of the clitoris. J Urol 174:1189–95.

Orr TJ, Hayssen V. 2020. Introduction to 'reproduction: the female perspective from an integrative and comparative framework'. Integr Comp Biol.

Orr TJ, Burns M, Hawkes K, Holekamp K, Hook K, Josefson C, Kimmitt A, Lipshutz S, Lynch K, Sirot L, et al 2020. It takes two to tango: including a female perspective in reproductive biology. Integr Comp Biol.

Pérez-Cerezales S, Ramos-Ibeas P, Acuña OS, Avilés M, Coy P, Rizos D, Gutiérrez-Adán A. 2018. The oviduct: from sperm selection to the epigenetic landscape of the embryo. Biol Reprod 98:262–76.

Perry JS. 1981. The mammalian fetal membranes. J Reprod Fertil 62:321–35.

Pollen JJ, Dreilinger A. 1984. Immunohistochemical identification of prostatic acid phosphatase and prostate specific antigen in female periurethral glands. Urology 23:303–4.

Schatten G, Schatten H. 1983. The energetic egg. Sciences 23:28–34.

Sloboda J, Zaviačič M, Jakubovský J, Hammar E, Johnsen J. 1998. Metastasizing adenocarcinoma of the female prostate (Skene's paraurethral glands). Pathol Res Pract 194:129–36.

Smith JA, WD Ross, (eds.). 1912. The works of Aristotle. Vol. 5. Oxford: Clarendon Press.

Suarez S. 2016. Mammalian sperm interactions with the female reproductive tract. Cell Tissue Res 363:185–94.

Tanghe S, Van Soom A, Nauwynck H, Coryn M, De Kruif A. 2002. Minireview: functions of the cumulus oophorus during oocyte maturation, ovulation, and fertilization. Mol Reprod Dev 61:414–24.

Terminologia Anatomica. http://terminologia-anatomica.org/en/Terms/View? sitemapItemId=275.

Tepper SL, Jagirdar J, Heath D, Geller SA. 1984. Homology between the female paraurethral (Skene's) glands and the prostate. Arch Pathol Lab Med 108:423–5.

Tregano AC, Epstein JI. 2018. Skene's glands adenocarcinoma: a series of 4 cases. Am J Surg Pathol 42:1513–21.

Tsutsumi S, Kawahara T, Hattori Y, Mochizuki T, Teranishi J, Makiyama K, Miyoshi Y, Otani M, Uemura H. 2018. Skene duct adenocarcinoma in a patient with an elevated serum prostate-specific antigen level: a case report. J Med Case Rep 12:32 (doi: 10.1186/s13256-017-1558-y).

van Anders SM, Goldey KL, Kuo PX. 2011. The steroid/peptide theory of social bonds: integrating testosterone and peptide responses for classifying social behavioral contexts. Psychoneuroendocrinology 36:1265–75.

Yoshizawa K, Ferreira RL, Kamimura Y, Lienhard C. 2014. Female penis, male vagina, and their correlated evolution in a cave insect. Curr Biol 24:1006–10.

Zaviačič M. 1999. The human female prostate: from vestigial Skene's paraurethral glands and ducts to woman's functional prostate. Bratislava: Slovak Academic Press.

Zaviačič M, Ablin RJ. 2000. The female prostate and prostate-specific antigen. Immunohistochemical localization, implications of this prostate marker in women and reasons for using the term "prostate" in the human female. Histol Histopathol 15:131–42.

Zaviačič M, Zajíčková M, Blažeková J, Donárová L, Stvrtina S, Mikulecký M, Zaviačič T, Holomáň K, Breza J. 2000. Ultrastructure of the normal adult human female prostate gland (Skene's gland). Anat Embryol 23:61.

Zukerman Z, Rodriguez-Rigau LJ, Smith KD, Steinberger E. 1977. Frequency distribution of sperm counts in fertile and infertile males. Fertil Stertil 28:1310–3.