Book Review

“Nether” No More: Bringing Genital Evolution to the Forefront


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Did you know that the male crane fly has a vibrator-like adornment on its penis? That female chickens eject more sperm after copulating with a low-ranking male than after copulating with a high-ranking male? Menno Schilthuizen, an evolutionary biologist at Naturalis Biodiversity Venter in Leiden and professor of evolution and biodiversity at Leiden University, the Netherlands, introduces the reader to a stunning array of genital adaptations in his book, Nature’s Nether Regions. He aims to convince the reader that animal—including human—genitalia comprise a wonderfully complex system resulting from a co-evolutionary tango between the sexes. Schilthuizen pursues this goal using an engaging and joyful writing style, expertly summarizing diverse research on the elegant complexity surrounding reproduction in animals and addressing how these processes and features might be reflected in the evolution of human genitalia.

Although the content of the book is complex and technical, Schilthuizen achieves the delicate balance between scientific prose and writing for a general audience. Beginning with a brief history of the study of genital evolution, he opens the first chapter with a seemingly puzzling statement: “This book is not about sex” (p. 9). In this opening section, he makes the case that a basic understanding and correct usage of biological terminology can open the door to a brilliant evolutionary show. He explains with great clarity why sex, fertilization, and reproduction are not interchangeable, and how sexual selection can build eccentric genitalia in males and females. By presenting these basic ideas and concepts at the outset, the reader does not need a background in evolutionary biology to enjoy and engage with Nature’s Nether Regions—just an interest in sex and genitalia.

Schilthuizen argues that genitalia are complex systems that did not evolve merely to deposit and receive sex cells. Using research examples from flies and birds to spiders and humans, he demonstrates that genitalia are often subject to intense selection pressures, which can produce astonishingly complex adaptations. Not only do male and female
genitalia evolve to optimize an individual’s own replicative success, but genitalia in one sex evolve counter-adaptations to adaptations in the other sex in a struggle to maintain control over reproduction. Indeed, female choice—before, during, and after copulation—is a powerful force in the evolution of genitalia. For example, the male mallard duck is equipped with a counterclockwise-coiled penis. As a counter-adaptation to reduce insemination by forced copulation, the female has evolved a clockwise-coiled vagina that the male can only fully penetrate if she relaxes her vaginal muscles, thus allowing her to favor the sperm of one male over that of another male (Brennan et al., 2007). In many species—including humans—females “dump” or retain less sperm in their reproductive tract that is inseminated by a disfavored male. Because of this, Schilthuizen proposes, males have a strong incentive to use their penis as an “internal courtship device” (p. 56), to persuade the female that he is a suitable mate. In a classic study by Baker and Bellis (1993), women who had an orgasm close to the time of their partner’s ejaculation retained more sperm in their reproductive tract. And it has also been documented that women partnered to more masculine men are more likely to achieve orgasm during copulation (Puts, Welling, Burriss, and Dawood, 2012), corroborating the hypothesis that human female orgasm—and perhaps female orgasm in mammals, generally—is a sire selection adaptation. Throughout *Nature’s Nether Regions*, parallel examples between animal and human genital evolution and its consequences are highlighted to demonstrate that humans fit seamlessly within the animal kingdom.

Schilthuizen presents sperm competition (Parker, 1970; Baker and Bellis, 1995) as a selective force contributing to the evolution of genitalia—the importance of which is sometimes overlooked in favor of cryptic female choice. Because of recurrent conflict between the sexes, genitalia co-evolve as a consequence of males competing for fertilization and females attempting to retain control of reproduction. Although sperm competition is widely recognized to occur in nonhuman animals, some researchers have been resistant to applying sperm competition theory to humans. Delightfully, Schilthuizen showcases research addressing human sperm competition in parallel to nonhuman research findings. For example, Schilthuizen reviews work indicating that the damselfly penis and the human penis both may have evolved features that facilitate the displacement of rival male semen from the female reproductive tract (Gallup et al., 2003; Waage, 1979). Other cross-species parallels of sperm competition are showcased in comparisons of humans with nonhuman primates. In the chimpanzee, for example, a portion of the ejaculate forms a relatively solid mucus plug following insemination. Similarly, in humans—as in gorillas—a portion of the ejaculate forms a gelatinous mucus plug following insemination. These mucus plugs may function to thwart sperm ejection by the female and to block subsequently inseminated rival male sperm from fertilizing ova (Dixson and Anderson, 2002).

Despite his appreciation that sperm competition may have been a recurrent feature of human evolutionary history, Schilthuizen is skeptical that the *human* penis, in particular, may have evolved to displace rival semen, yet subsequently comments that penile adaptations for semen displacement are “probably quite widespread” (p.117) in the animal kingdom. He argues that because the chimpanzee penis is smooth and unable to displace sperm, it is unlikely that the human penis evolved to do so, given that chimpanzees are notably more promiscuous than humans. This is a problematic analysis, however. Throughout the book, Schilthuizen highlights the complexity of genitalia throughout the
animal kingdom and emphasizes that closely related species often evolve strikingly different genitalia. Moreover, he presents research that indicates that the type of mucus plug—on a continuum from solid to gelatinous—produced by nonhuman primates and humans varies with the promiscuity of the species. Consequently, the level of sperm competition in a species affects features of adaptations designed to block or to compete with rival sperm. Thus, it is possible, for example, that the human penis evolved differently from the chimpanzee penis in that adaptations for semen displacement evolved in humans because the human mucus plug less effectively blocks subsequent inseminations by rival males. Conversely, chimpanzees may not have evolved semen displacement penile adaptations because they produce a relatively solid plug that more successfully blocks subsequent rival male ejaculates from navigating the female reproductive tract. Thus, different genital adaptations may have evolved in humans and in nonhuman primates due to the strength of selection pressures imposed by the different levels of sperm competition in these species. Additionally, research has documented various psychological adaptations in humans, such as mate guarding tactics (Buss and Shackelford, 1997) that men deploy to combat sperm competition and to maintain their partner’s fidelity.

Despite these quibbles, Schilthuizen’s recognition and discussion of sperm competition as an important force of genital evolution is refreshing and encouraging. *Nature’s Nether Regions* changes the landscape by showcasing how sperm competition is of equal importance to female cryptic choice in the scientific study of genitalia, sex, and reproduction. In particular, the chapter entitled *Future Suitors* provides insightful discussions on the ways in which sperm competition can be applied to humans. For example, Schilthuizen discusses the rapid evolution of male seminal fluids, fostering avenues for future research on the properties of human semen that facilitate fertilization, the ability of the human vagina to absorb chemical constituents of seminal fluids, and the possibility that men can induce ovulation in women.

In the closing chapter, Schilthuizen highlights several implications of research findings on genital evolution. He emphasizes that copulation and reproduction do not necessarily represent cooperation between males and females, but instead that these processes reflect a recurrent and intense co-evolutionary arms races between the sexes. Consequently, genitalia evolve rapidly—indeed, they are among the fastest-evolving traits in the animal kingdom—and elaborately, often resulting in extravagant structures crafted for function and form by sexual selection. Schilthuizen closes the book with the argument that genital evolution may be a driving force in the origin of new species. He argues that rapidly evolving dual-adaptations could cause a splitting of species by imposing barriers to reproduction. Arguing that genital evolution might be responsible for the origin of species highlights the theoretical and empirical harvest to be reaped by research on genital evolution.

A central aim of *Nature’s Nether Regions* is to convey to the reader that genitalia and genital evolution are not only fascinating, but also worthy of scientific study. Research on genital evolution promises important implications not only for understanding animals, but also for understanding humans. Moreover, Schilthuizen argues successfully that research on genital evolution can provide broad insights into evolution by sexual selection and biodiversity, generally. Striking the elusive balance between engaging writing and scientific accuracy, *Nature’s Nether Regions* is a literary treasure for anyone fascinated with evolution, sex, and reproduction.
References


