THE EVOLUTION OF HOMO LUDENS: SEXUAL SELECTION AND A THEOLOGY OF PLAY

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Abstract. This essay argues that reflection on sexual selection can be theologically generative, and that it presents needed counteremphases to some of the discussions about theological anthropology that have been fueled by theological reflection on natural selection. It introduces sexual selection and provides an overview of different approaches to sexual selection found within evolutionary biology today, before transitioning to a reflection on one theologically relevant insight from sexual selection—namely, the importance of play. It argues that the mating and play behaviors of animals reveal the noncompetitive relationship between necessity and gratuity, and thus provide theologians with an example of grace building upon, and not destroying, nature. While play is sometimes depicted in philosophical and theological accounts as the achievement of culture that supersedes the mundane necessities of nature, sexual selection can also help to illuminate the ways in which culture is dependent upon nature, and play is a thoroughly natural phenomenon that provides resources for human cultural elaboration.

Keywords: evolutionary biology; natural selection; play; theological anthropology; theology and science

“Play, or rather sexual display, is predominant in animal life precisely at the mating season. But would it be too absurd to assign a place outside the purely physiological, to the singing, cooing, and strutting of birds just as we do to human play?”

—Johan Huizinga (1949, 9)

Introduction

The field of Science and Religion has taken seriously the ramifications of evolutionary biology for theological anthropology, and a predominance of this literature has focused on natural selection and its implications for human nature. Is nature “red in tooth and claw”? Do the principles of
natural selection reveal that humans are naturally violent and selfish, and if so, what does this mean for traditional Christian doctrines like the *imago Dei*, the Fall, original sin, and the problem of evil? More recent trends in the Science and Religion literature have emphasized the ways in which cooperation and “altruism” (variously defined) are fundamental to evolution. These investigations have been enormously generative for Christian theology, and they have prompted us to rethink many of our assumptions about what it means to be creatures living in an evolutionary milieu.

However, I suggest in this article that we have not sufficiently explored Darwin’s “other” theory of evolution—evolution by sexual selection—and its implications for theological anthropology. I propose that reflection on contemporary debates in sexual selection can be theologically generative, and furthermore, that reflection on sexual selection can provide needed counteremphases to some discussions in theological anthropology that have been fueled by reflection on natural selection. In addition to investigating the extent to which humans and other creatures have evolutionary histories of violence and selfishness (and sexual selection can also reveal these aspects of creaturely life), sexual selection also prompts us to ask—what does it mean for theological anthropology if creaturely life as we know it has emerged from an evolutionary history defined by playfulness and pleasure? Sexual selection theories reveal a material and evolutionary world pervaded by esthetic abundance that exceeds “the bare requirements for existence” (Grosz 2008, 6). It invites us to recall the fundamental importance of pleasure and play for human flourishing, and it reminds us that the nature of creaturely life is oriented toward far more than just survival and the perpetuation of genes. Yet, there is an even deeper theological principle revealed by the workings of sexual selection. In reflecting upon the mating and play behaviors of creatures, theologians are given an example of the ways in which gratuity does not compete with utility; rather, the gratuitous in nature builds upon the useful or necessary. Sexual selection can help to reveal that the “bare requirements for existence” already include the gratuitous, the pleasurable, and the playful, and so as we might say in a theological key—nature is always already graced. Furthermore, though play is sometimes depicted in philosophy and theology as the achievement of culture, sexual selection can help to illuminate the extent to which play is a natural phenomenon that provides resources for cultural elaboration. Through the study of sexual selection, we can also perhaps be led to encounter the playful God who continually evokes our desires to draw us more deeply into communion with God and with one another. I begin then with an introduction to the history of sexual selection theories and an overview of the different approaches to sexual selection found within evolutionary biology today, before transitioning to a reflection on the possibilities for theological engagement with sexual selection.
Historical Developments in Sexual Selection Theories

Darwin is most famous for his theory of natural selection. Less well known and understood, however, is his theory known as “sexual selection,” a theory that he viewed as distinct from, but entangled with, natural selection. If natural selection was a theory about competition for survival, Darwin saw sexual selection as a theory about competition for reproductive success and access to suitable mates. He describes sexual selection as “the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction” (Darwin [1871] 1981, 256). Darwin theorized that sexual selection works primarily in two ways, either through “contests of attractiveness” or “contests of strength,” or in other words, through courtship or battle (West-Eberhard 2014, 503). As Darwin understood sexual selection, a male could find reproductive success either by wooing a female or by defeating his rivals for the female in combat. He suggests that features such as “weapons of offence and the means of defence possessed by the males for fighting with and driving away their rivals—their courage and pugnacity—their ornaments of many kinds—their organs for producing vocal or instrumental music—and their glands for emitting odours” are likely the result of sexual selection pressures since they serve only to “allure or excite the female” (Darwin [1871] 1981, 258). He proposed then that striking traits that seem to be otherwise maladaptive could persist in being transmitted to the next generation simply because they were perceived as attractive. These seemingly detrimental traits could ultimately provide an advantage in making it more likely that the male would win the favor of the female and thus be able to reproduce.

Darwin viewed sexual selection as an essential companion theory to natural selection because he thought that it could help to explain the presence of features that persist in species but do not have obvious advantages in terms of helping the species compete for survival. A frequently cited example of a feature that would seem to disadvantage an organism but that persists in the species is the plumage of the male peacock, which perplexed Darwin greatly. As Fine summarizes, “if a primary goal of your life is to avoid being eaten by another animal, then a large eye-catching, wind-dragging, feathered rear sail is not an asset” (Fine 2017, 30). Developing his theory of sexual selection in his Descent of Man, Darwin states

Courage, pugnacity, perseverance, strength, and size of body, weapons of all kinds, musical organs, both vocal and instrumental, bright colours, stripes and marks, and ornamental appendages, have all been indirectly gained ... through the influence of love and jealousy, through the appreciation of the beautiful in sound, colour, or form, and through the exertion of a choice. (Darwin [1871] 1981, 402)

Here, Darwin argues that sexual selection exercised through esthetic taste, desire, affective realities such as love and jealousy, and the social choices of
organisms play profound roles in shaping the direction of species evolution. As Hoquet argues, for Darwin, “sexual selection opens up the possibility of an aesthetic sensibility and suggests that beauty somewhat determines animal anatomy and behavior” (Hoquet 2015, vi). In articulating this view of sexual selection, Darwin suggests that organisms are not passive objects upon whom the mechanisms of natural selection work, rather, they participate in their evolution through their sexual, social, and esthetic choices and habits. Furthermore, Darwin argued, females play a key role in influencing the development of species through their choices of mates, leading him to express in surprise, “It could never have been anticipated that the power to charm the female has sometimes been more important than the power to conquer other males in battle” (Darwin [1871] 1981, 279). For Darwin, evolution is in part driven by the explosive unpredictability of the delights and pleasures of organisms, by their appreciation of beautiful forms and sounds, and by the agency of females.

Darwin’s arguments about sexual selection were opposed by many following the publication of *The Descent of Man*. For example, biologist Mivart argued in 1871 that sexual selection as understood by Darwin, with its emphasis on the important role played by female choice, could not lead to the evolution of complex traits because of the “instability of vicious feminine caprice” (Mivart 1871, 59.) It is worth noting that the meaning of the terms *vicious* and *caprice* has both shifted since the nineteenth century. As Richard Prum notes,

In our modern sense, the word vicious means deliberately violent, nasty, or dangerous, but its original meaning was immoral, depraved, or wicked … Caprice has come to refer to an entertaining fancy or light-hearted whim, but its original meaning was a prompt, arbitrary turn of mind made without apparent or adequate motive. (Prum 2015, 241)

The point remains that Mivart believed female organisms to be incapable of exerting esthetic choice. Mivart and another prominent biologist at the time, Alfred Russel Wallace, also agreed that nonhuman animals could not possess what they believed was a singularly human capacity—esthetic discernment (Prum 2017, 32). Both Mivart and Wallace viewed sexual selection as simply natural selection manifesting in a different way—the seemingly gratuitous can be explained by its utility. What we consider beautiful in nature, according to them, is simply an indicator of an organism’s adaptive fitness. Beauty provides reliable information about the quality of the organism in terms of its ability to survive (Cronin 1991, 186). Wallace and Mivart provided a precursor to the “good genes” model of sexual selection that is prevalent today, although they would not have used the language of genes. Wallace, for example, spoke instead about how esthetic traits are eventually always useful to their bearer, and are therefore indicators of vigor and vitality. The Mivart-Wallace view of sexual
selection as simply a mechanism of natural selection became the prevailing view in the years following the publication of *The Descent of Man*, and as we will see, it largely remains so to this day, with some notable exceptions.

**Contemporary Debates about Sexual Selection**

Questions about how sexual selection works and what drives mate choices are hotly debated within evolutionary biology circles. The divergences in interpretation of sexual selection also illuminate the broader philosophical frameworks within which particular scientists work.

**“Good Genes”**

The notion that flashy or esthetically beautiful traits are indicators of adaptiveness and that they are selected in order to perpetuate high-quality organisms has been the most prevalent understanding of sexual selection since the time of Darwin. Proponents of the “good genes” school of thought argue that “mate choice evolves under selection for females to mate with ecologically adaptive genotypes” (Kirkpatrick 1987, 44). In this framework, an organism’s beauty or ornamentations are thought to provide honest signals about the organism’s quality. Within the “good genes” school of thought, sexual selection is natural selection working in a different way. What may appear to us as gratuitous beauty in nature can be explained through its utility in this view. The “good genes” model of sexual selection perhaps endures with such persistence because, in the words of Gil Rosenthal, “it most appeals to our folk eugenic sensibilities” (Rosenthal 2017, 406). Roughgarden argues similarly that the standard “good genes” model of sexual selection “underwrites ‘genetic classism’ by naturalizing a mythical urge on the part of females to locate and sleep with males who have the best genes. Sexual selection is a narrative of genetic entitlement” (Roughgarden 2009, 4).

**Esthetic Evolution**

As Kirkpatrick notes, the nonadaptive or “esthetic” model of sexual selection “holds that preferences frequently cause male traits to evolve in ways that are not adaptive with respect to their ecological environment” (Kirkpatrick 1987, 44). Prum, a well-known advocate of this view, argues that traits evolve simply because they are attractive to mates and that they do not necessarily indicate greater adaptive success, although they can accidentally reveal quality (Prum 2017, 11). As Prum argues, sexual selection is “more like art—it’s about beauty and aesthetic choices” (Prum 2019). For Prum, then, the seemingly gratuitous beauty found in nature is indeed, in most cases, gratuitous and arbitrary. He does acknowledge that flashy traits could potentially, in a hidden way, provide honest signals about the good
genes of the mate. As he notes, “After all, a Maserati or a Rolex can be aesthetically pleasing while also performing utilitarian functions like driving at race car speeds or keeping accurate time” (Prum 2017, 73). However, the striking traits of organism should not be primarily interpreted as useful tools for survival; instead, they are the gratuitous and arbitrary result of the instability of creaturely desire. According to this school of thought, sexual selection can be distinguished from natural selection, and sexual selection can work in ways that are even oppositional to natural selection.

Sexual Selection and Play

Roughgarden suggests a third option for how to characterize the nature of organism mate choices and reproductive behaviors. While she acknowledges that her theory fits broadly under the category of “sexual selection research” (Roughgarden 2009, 18) (though she discourages categorizing it as such because she thinks it may be confusing), she argues that standard sexual selection theories are “always mistaken” (Roughgarden, Oishi, and Akçay 2006, 965) and should be replaced by what she terms “social selection.” Roughgarden’s critique of sexual selection theories is multifaceted, but one of her central challenges concerns “the scientific validity of a world view that naturalizes selfishness and sexual conflict” (Roughgarden 2009, 4). She is concerned that sexual selection theories have used biology to “develop a philosophy of universal selfishness, conflict, and lack of empathy,” and further, she believes that these theories fail to accurately describe the reality of the biological situation (Roughgarden 2009, 5). Females do not choose males because of genetic quality or because of an arbitrary “female esthetic,” according to Roughgarden, Oishi, and Akçay (2006, 965). Instead, they argue, animals work together to produce the greatest number of offspring that they can because, they argue, “offspring are investments held in common” (2006, 965). Reproductive social behaviors of animals, then, should be understood in terms of cooperative “teamwork” (Roughgarden 2009, 13).

Cooperative teamwork involves animals sharing a common interest and they work together to achieve evolutionary “payoffs” or benefits. The work of the team is cooperative not only in the sense that it results in a mutually beneficial outcome, but the “way the game is played,” or in other words, the “process of perceiving and playing the game” is also by its nature cooperative (Roughgarden, Oishi, and Akçay 2006, 966–67). Cooperation can, of course, sometimes fail, in which case conflict and competition may arise, but these are derivative of the fundamental cooperation that motivates most animal reproductive social behavior. Cooperation in mating and reproductive behaviors of animals should thus be thought of as “coordinated play that furthers a team goal” (Roughgarden 2006, 113). Flashy traits, according to this framework, do not serve as honest signals of genetic
quality, nor are they the result of arbitrary female esthetic taste. Rather, striking features like the tail of the peacock serve as “admission tickets to monopolistic resource-controlling coalitions” (Roughgarden, Oishi, and Akçay 2006, 968). Failing to have the ticket typically results in exclusion or prejudice. In other words, Roughgarden suggests that flashy traits—in males and females—may allow an animal to gain access to “power-holding cliques” that control opportunities for the successful raising of progeny (Roughgarden 2009, 242).

Roughgarden’s theory is useful in that it also provides an evolutionary explanation for the pervasive presence of nonreproductive intimate behaviors among animals such as same-sex copulation, mutual grooming, cosleeping, interlocking vocalizations, and other nonreproductive intimate behaviors. The purpose of these nonreproductive intimate behaviors are, according to Roughgarden, to “coordinate actions and tacitly to sense one another’s welfare” (2009, 243). These behaviors also have an evolutionary payoff—pleasure and bonding. Pleasure in physical intimacy deepens relational bonds and strengthens connections. It also contributes to effective teamwork, Roughgarden argues. Thus, pleasurable and playful behaviors, while not strictly “necessary” from a reproductive point of view, are evolutionary useful in promoting more effective teamwork to achieve shared goals. The more deeply bonded the pair is, the more successful they will be in working together to rear their offspring. Pleasure and play are gratuitous, then, in the sense that reproduction could happen without them. However, they are evolutionarily useful behaviors that make the ultimate goal of reproduction—raising offspring—much more likely to be achieved.

We have now briefly examined the history of sexual selection theories, particularly in the work of Charles Darwin, while also considering contemporary debates about the nature of sexual selection. Roughgarden's articulation of a theory of “social selection,” meant to replace standard accounts of sexual selection that naturalize selfishness and conflict, depicts animal mating behaviors as a type of cooperative game in which players work together to achieve shared goals. The “game” of mating and reproduction, according to this theory, is more effectively played when the players find pleasure in one another and form effective bonds that enable them to track one another’s welfare and to coordinate their actions more smoothly. Mating is thus a type of “playing” among animals that illuminates the noncompetitive relationship between what is useful in nature and what is gratuitous. The seemingly gratuitous is also useful. This could be interpreted in a reductionist way as collapsing meaningful categories like love, intimacy, friendship, play, and pleasure into “mere survival” techniques. On the other hand, it could be read as revealing the brilliance of evolutionary processes that ensure that those things in life that are the most pleasurable and meaningful—intimacy, play, love, and
friendship—are also deeply useful for the ongoing flourishing of species. The mating and play behaviors of animals undermine a contrasting or competitive relationship between the gratuitous (the realm of grace) and the natural (the realm of necessity).

We turn now to consider philosophical and theological accounts of play before considering in the final section how sexual/social selection theories can enrich theological accounts of play.

Theology and Play

The idea of play as an activity that is befitting of humans especially in light of our relationship to the divine appears in the writings of Greek thinkers who would exert significant influence on the development of Christian theology—Plato, Aristotle, and Plotinus. In some of this literature, play is depicted as appropriate for human life since humans exist because of the creative work of the divine and are the playthings of the gods. In contrast to a biological account of play as we have seen above, play in this context is “natural” for humans because of the nature of their relationship to the divine. Plato, in his *Laws*, articulates this notion of humans as toys of the gods. He has the “Athenian” interlocuter state:

I maintain that serious matters deserve our serious attention, but trivialities do not; that all men of good will should put God at the center of their thoughts; that man, as we said before, has been created as a toy for God; and this is the great point in his favor. So every man and every woman should play this part and order their whole life accordingly, engaging, in the best possible pastimes—in a quite different frame of mind to their present one.

(Plato [340s BCE] 1997, 803b-c)

Plato then has the Athenian interlocuter clarify that every human should spend life “at play (παίζωντα)—sacrificing, singing, dancing—so that he can win the favor of the gods and protect himself from his enemies and conquer them in battle” (Plato 1997, 803e). Plotinus echoes Plato as he argues, that humans are “living toys” (ζωντα παιγνια) (2019, III.2.16), though, as Rahner notes in his commentary on this passage from the *Enneads*, the human is at the same time “more than a mere token which can be moved or thrown away in play as an unpredictable mood may dictate” (Rahner 2019, 35). For Aristotle, and this is developed later by Aquinas, play is essential to the virtuous life. As he argues in The *Nicomachean Ethics*, “Since life includes rest as well as activity, and in this is included leisure and amusement, there seems here also to be a kind of intercourse which is tasteful … evidently here also there is both an excess and a deficiency as compared with the mean” (Aristotle [fourth century BCE] 2009, 1128a). He then contrasts the “buffoon” (ὁ βωμοιολόχος) who never ceases to play and turns everything into a joke, with the “boor” (ὁ ἄγροικος) who never makes a joke and cannot tolerate being around
those who do (Aristotle [fourth century BCE] 2009, 1128a). The virtuous person is the “ready-witted” person (ὁ ἐυτράπελος), one who is able to “turn this way and that,” or in other words, one who has a type of flexibility of personality such that she is able to enjoy amusements and pleasures without indulging in an excess of frivolity (Aristotle [fourth century BCE] 2009 1128a).

Aquinas reflects on play in his commentary on Aristotle’s *Nicomachean Ethics*, as well as in his *Exposition of the “On the Hebdomads” of Boethius* and in the *Summa Theologica*. In the *Commentary on Aristotle’s Nicomachean Ethics*, Aquinas notes in agreement with Aristotle that amusement is a good of the human life. He states, “As man sometimes needs to give his body rest from labours, so also he sometimes needs to rest his soul from mental strain that ensues from his application to serious affairs. This is done by amusement” (Aquinas [13th c. BCE] 1993, §851). In his *Exposition of the “On the Hebdomads” of Boethius*, Aquinas compares the contemplation of Wisdom with play (ludo). This comparison is justified, he argues, “because play is delightful (delectabilis) and the contemplation of Wisdom possesses maximum delight,” and “because things done in play are not ordered to anything else, but are sought for their own sake, and this same trait belongs to the delights of Wisdom” (Aquinas [13th c. BCE] 2001 5). Finally, in his *Summa Theologica*, he argues, “Now just as weariness of the body is dispelled by resting the body, so weariness of the soul must needs be remedied by resting the soul: and the soul’s rest is pleasure … the remedy for weariness of soul must needs consist in the application of some pleasure, by slackening the tension of the reason’s study” ([13th c. BCE] 1920, II.II, q 168, a. 2). Aquinas portrays play as “natural” for humans as a form of rest from work, and proper playfulness as key to the virtuous life. In his comparison of play with the contemplation of divine Wisdom, he dignifies the role of play. Thus, for Aquinas, play expresses something central to theological anthropology. Play is a serious matter. Beyond simply providing a respite from work for the sake of doing more work (although this a part of its value), play enables us to encounter our yearning to reach out beyond ourselves, the same yearnings that prompt us to seek communion with God.

Rahner addresses the importance of a theology of play from the perspective of historical theology in his short monograph from 1964 entitled *Der Spielende Mensch* (*Man at Play*). In this text, he critiques the “barren solemnity of a purely utilitarian life,” and argues that the man who is able to play is “man at his highest level of cultural development” (Rahner 2019, 4 and 7). A true understanding of *Homo ludens*, he argues, can only be attained via an appreciation for *Deus ludens* who called the world into being not out of necessity, but rather, “as part of a gigantic game” (Rahner 2019, 10). He recalls imagery from Maximus the Confessor and Gregory of Nazianzus, who refer to the Incarnation of the Divine Logos as play.
The Logos on high, says Gregory, ‘plays (παίζει) in all sorts of forms, mingling (κιένας) with his world here and there as he so desires’ (1857, 624a13–25a1). Maximus repeats and reflects on this quote from Gregory in his *Ambiguum* 71. The playing human then, according to Rahner, imitates the playful God whose love and delight overflow into free acts of creation and incarnation. Creation becomes a theatre for the “game of grace,” and the knowledge that God’s acts of creation and incarnation emerge from freedom and love and are not bound by necessity, enables the human to play, Rahner argues, because she can see herself as one whose life has meaning and whose existence is not necessary but which has emerged as a product of God’s delight (Rahner 2019, 36). To be a *Homo ludens* is not to ignore or minimize the tragic elements in the world, he notes. Instead, the *Homo ludens* is at the same time a “man of tragedy … for he sees through the tragically ridiculous masks of the game of life and has taken the measure of the cramping boundaries of our earthly existence” (Rahner 2019, 37). The human with no appreciation for tragedy would become Aristotle’s βωμολόχος (buffoon), who sees everything as a joke, but the person who comprehends the dual nature of life as both comedic and tragic becomes the *Homo vere ludens* and the *ludimagister* (Rahner 2019, 4–5). Ultimately, in Rahner’s framework, the true nature of human play is best exemplified in the playing of the Church, which anticipates the “great festival of heaven” (Rahner 2019, 62).

**Theology, Play, and the Evolution of Homo Ludens**

From this reflection on theologies of play within the Christian tradition, we return to the theories of sexual selection explored earlier in this article to investigate the extent to which they enable us to expand this conversation. Investigating sexual selection reveals in ways not so far unearthed by our philosophical and theological interlocutors the material, organic, and evolutionary underpinnings of the impulse to play that make human creativity and playfulness possible. Regarding Rahner’s notion of play as the height of human culture, sexual selection reminds us that play is deeply rooted in our evolutionary history, and it serves important biological purposes in terms of developing pair bonds and facilitating cooperative teamwork in various species. Play is natural; it is shared with many species; and it reveals the extent to which culture is always deeply entangled with—and indebted to—nature. Play is not gratuitous to the exclusion of the necessary—rather, the gratuity of play contributes to the necessities of nature. Nature and grace are not in competition.

Furthermore, while both Aquinas and Rahner refer to play as the outworking of human freedom, sexual selection nuances this point. From the perspective of sexual selection, play is free in the sense that it is, in part, gratuitous, uncalculated, and somewhat unpredictable (though sometimes
play can follow quite strict rules). However, play is not free in the sense of being completely unconstrained or disconnected from the broader evolutionary milieu and history in which we are immersed. This is also true of creaturely agency in general—the choices we make and our actions in the world are meaningful but never disconnected from environmental and evolutionary influences. The playing we do today is therefore always a type of riffing on the play of those who have come before us.

This reading of sexual selection as the realm of play and creativity is not meant to minimize or obfuscate the reality of violence, coercion, and cruelty that also exist in our evolutionary history. Rather, as I stated in the introduction, it is meant to compliment and be read alongside theological reflection on sin and violence. As Rahner noted, one must be able to hold together both the comedic and the tragic in life in order to be Homo vere ludens.

Play is a privileged site at which the noncompetitive relationship between the necessary and the gratuitous is revealed. The creature who plays affirms the superabundance of the world: the resources in the natural world transcend what is needed merely for survival. Yet, the gratuity of play also contributes to a creature’s ability to meet the basic needs of their life. The activities of play require us to encounter anew the animal, the earthly, and the organic forces that pulsate within us. In the playfulness of creatures that permeates the world as revealed by sexual selection, we can perhaps catch glimpses of the wide scope of the delight of the God who “plays (παίζει) in all sorts of forms, mingling (κυρνάς) with his world here and there as he so desires” (Gregory of Nazianzus (624a13–25a1).

Note
1. Darwin expressed his confusion about traits that cannot be explained by the normal processes of natural selection in a letter to Asa Gray. He writes, “I remember well the time when the thought of the eye made me cold all over . . . now small trifling particulars of structure often make me very uncomfortable. The sight of a feather in a peacock’s tail, whenever I gaze at it, makes me sick!” (Darwin [1887] 1958, 244).

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