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The Evolution
of Sexuality

Evolutionary Psychology

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The Evolution of Sexuality

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Foreword

Those buzzes… Forget the short-sighted funding agencies, snail-paced build-up of data, not-quite-significant results, hung-over students, and empty conference theaters. Remember instead the thrill of a new angle, a new field, an inspired student, a successful protégé, a new collaborator, new funding, a big breakthrough—Eureka! These are the moments that keep us going. These are the ones that make us glad we are scientists and, in the case of the contributors to this volume, that make us glad we work on the Evolution of Sexuality. Such buzz-moments are magical. Every one of us has a list and most need little encouragement to reminisce their way through that list until somebody shuts us up. But as the invited writer of the Foreword to this volume I have carte-blanche—so for the next 100 pages…

Sometimes I feel that I have lived through the whole evolution of the Evolution of Sexuality; that I was there at the big bang. I was not of course. Darwin had found a few words to say on the matter long before my time. Even so, as a Zoology undergraduate in the early sixties I found no such subject being taught or even envisaged. At Bristol as in most places, evolution meant phylogeny, genetics meant what Mendel did with his peas, sex was the structure of reproductive systems plus maybe eggs, and behavior was not quite nice and was an art-subject taught by psychologists. But even before I graduated something was stirring—and luckily for me there was somebody in my year-class at Bristol who shared my excitement.

Geoff Parker and I were very different characters, yet around 1964 we both found a lifetime's inspiration from a single controversy. Outside of Bristol a war was raging in the world of evolutionary theory, triggered by V. C. Wynne-Edwards' 1962 book extolling the power of group selection to bring about evolutionary change. People were taking sides, even in Bristol, with Geoff and I aligning with what seemed to be the minority at the time, the Individual Selectionists. In a bar or a refectory we would defend our cause against all-comers. We would even go to the then-extreme of claiming individual selection to be a force in the evolution of behavior. It was our first experience of the buzz to be gained from the defending of an academic idea that, apparently, was outrageous. At a time when few believed that behavior of any sort was even heritable, our backs were against the wall for much of the time.

Over the course of the postgraduate years that followed, Geoff was destined to spend much of each summer sleeping in the back of a van in the English countryside, all the better to watch the first cowpats dropped each day in nearby fields. But before that, during the first long winter of 1965–1966, we shared a freezing apartment on the outskirts of Bristol. There, on those nights that we were both in, we would sit bent over the single gas fire, singeing gas-tainted toast on long forks and talking about sex—as postgraduates do. Unlike most postgraduates, our conversations revolved around dung-flies and Geoff's ground-breaking notion of sperm competition. It is fun to think that for those few months that fire-lit room in Bristol could have been the only place in the world where sperm competition was being discussed. But even that early in the subject's existence we did from time to time dare to ask… We did wonder… We did talk about how… But our conclusion was always the same: "It can't be done, can it?" And we would go back to talking about dung-flies. Or—another favorite sexual topic because it seemed so impenetrable—we would agonise over why there were two sexes, and only two. That question really stumped us, maybe even shook our faith a little. How could such a question possibly be answered by individual selection?

Soon we discovered that we were not alone in our excitement over evolutionary questions about behavior. Outside of Bristol it seemed that increasingly, and reassuringly, even quite rational people were becoming just as excited. Traditional zoologists still did not consider such questions quite scientific or even quite decent. They still considered them primarily the domain of psychologists. But everywhere new generations of academics were forging cross-discipline links—and following a deadly bite from a virulent Patas Monkey that "everywhere" came to include Bristol.

Until 1965 the Head of the Department of Psychology at Bristol had been Professor Ronald Hall. But on his return from a field-trip to Africa collecting data on wild primates, he was bitten by a member of a troop he had established in captivity. Whatever the infective agent, it was obscure and lethal and Ronald Hall sadly died from the bite, leaving a large section of his department in disarray. To reorient themselves, his orphaned group began holding weekly seminars to discuss each other's interests and to find a new direction. And hearing that Geoff and I might be receptive to an evolutionary approach, they invited us to attend.

Those meetings were a revelation to us all, a first faltering taste of the discipline that was to become "Evolutionary Psychology" in Psychology and "Behavioral Ecology" or "Sociobiology" in Zoology. The atmosphere at the seminars was amazing, and we all quickly became zealots. It really did feel as though we were on the verge of a new and exciting field. Some of the subject's pioneers came to attend and talk. Hans Kruuk, for example, who took us through the observational and experimental methods he was developing to ask evolutionary questions about lion behavior in the Serengeti. The main focus of the group was social behavior, mainly in birds and mammals, but that inevitably involved sexual behavior too. And whenever possible we swung the talk round to the question that interested us all: could we really apply the same evolutionary approach to humans? Few thought it possible or even, in a career sense, desirable, and at the time it seemed just a dream. It was an

exciting dream though—and in 1967 that dream took a major step nearer to reality. *The Naked Ape* appeared.

Desmond Morris' book was dynamite, blasting its way into people's consciousness. Love it or hate it, everybody had an opinion on it. And for those of us desperately seeking reliable ways to apply evolutionary principles to behavior the book served two great purposes. First, it jettisoned into academic and public arenas alike how much could be gained from discussing *Homo sapiens* as just another animal. And secondly, it demonstrated clearly how not to do it. Pitfalls existed, and Desmond, with whom I was to collaborate on projects more than once in the years to come, had fallen into many. His book was a brilliant catalyst, but also a stark warning of the mistakes that could be made.

After *The Naked Ape*, what budding zoologist/psychologist would not be interested in the evolution of human sexuality? I never even contemplated the possibility as I moved from Bristol to my first temporary teaching post at the University of Newcastle upon Tyne—but I was in for a shock. From the euphoria of the evolutionary ethos at Bristol, I felt I had stepped back into the Dark Ages. My nemesis came in the form of the Department's resident palaeontologist who insisted that the only truly scientific way to study evolution was via fossils. And as fossils patently did not behave his stance was that there was no point even contemplating the matter—and he suggested quite forcefully to our mutual students that they should ignore everything I said on the subject. Perhaps because he was established and respectable and I apparently was neither, he generally held sway. I could see the suspicion in my tutees eyes as armed with copies of Desmond's book I tried to get them as excited about the questions raised as I was. It was hard work, leaving me feeling more like a smutty miscreant than a motivator.

Fortunately, not all of my students at Newcastle were so easily swayed by enemy propaganda. Officially, I was being employed as an entomologist and among the undergraduates in one series of my Entomology lectures in the early 1970s was a man destined to pioneer the study of a whole field in the evolution of sexuality. Professor Tim Birkhead of Sheffield University has kindly said or written more than once that it was my lectures on Geoff Parker's sperm competition work on dung flies that inspired his choice of career and research direction. Admittedly, after well over a decade of friendship, Tim and I did later cross swords and harsh words have been written and said. But none of that conflict can erase the pleasure and pride I took from the early years of seeing him opening up the whole study of sperm competition in birds.

Newcastle brought another buzz moment. In a single memorable phone conversation with Geoff Parker, by then at Liverpool, I discovered that we had both dreamed-up a solution to our long-standing niggle at the conundrum of two sexes. The answer, we had both decided, had little to do with maleness and femaleness and everything to do with eggs and sperm. Explain the evolution of anisogamy, we encouraged each other, and everything else would fall into place. Computer modelling was the obvious tool and Geoff was just the person to do it—and he did. He has since improved on that original 1972 *Journal of Theoretical Biology* paper of ours—but as far as I know the main principle still stands. And as that question was

one of the first that he and I had jointly battered our brains against while toasting bread in a freezing flat, I still get a surge of excitement when I remember the phone call that initiated our laying it to rest.

In 1975, I moved from Newcastle to a permanent position in Zoology at the University of Manchester. Many more buzz-moments lay ahead though not all involved the evolution of sexuality—but those that did more or less defined the final phase of my academic life and made those years by far the most exciting and rewarding of all. Although still partly an entomologist and by then also an ornithologist I was taken on at Manchester mainly to teach Behavioural Ecology. The subject was still very much in its infancy. It would be another 6 years before John Krebs and Nick Davies published their now-classic introduction to the subject. Even Richard Dawkins' *The Selfish Gene* was still a year from appearing. So I had considerable freedom over what to teach and how to teach it. I did dutifully cover everything considered mainstream at the time, but I also indulged myself in a lecture or two by asking "what if" we could study human behavioral ecology in the same way as for other animals.

I made no secret during those lectures of the fact that I thought human sperm competition would be a fantastic subject area. "Totally impossible to study, of course," I would say, "unless one of you…" and I would wave my hand around the class "…can think of how it could be done." I had probably made that gesture and said those words 6 or 7 years in succession before, by chance, there was a man present who had been a medical student for a while before deciding he preferred zoology. He thought he did know how it could be done and came hot-footing to my room soon after to tell me so. His name was Mark Bellis.

I shudder to think how many curries and units of alcohol Mark and I consumed over the next few months and years as we discussed possibilities, ways and means, and where it all could lead. Maybe we also discussed safety and ethics—but I doubt it. Our investigations began in an age when "just be sensible" was the only mantra for safety, and if ethical committees existed they had no real muscle—which was just as well if a particular External Examiner to our Department a year or two into our work was typical. This man refused even to discuss one of our student's projects in her viva and reduced her to floods of tears by calling her a "painted whore". Her crime? Collecting copulatory ejaculates from pairs of volunteers who although cohabiting were unmarried. If Mark and I had tried to start our work even just 10 years later… Well, we probably would not have been allowed to start at all.

Those early years were a whirl of discussions, arguments, and inspirations; so many eureka moments crammed into such a short time that who-first-said-what was soon lost in leaky memories. We cannot even remember with certainty which of us dreamed up our Kamikaze Sperm hypothesis. My main contribution to the cauldron from which we fished the idea stemmed from a cocktail party thrown in London in 1981 by the adorably eccentric Dame Dr Miriam Rothschild. An expert on fleas and an enthusiastic lepidopterist she had invited all 44 of the speakers from a special *Biology of Butterflies* symposium organized by the Royal Entomological Society of London. Difficult though I find it to believe now, I was one of those speakers—talking not about sex but migration. At that party, over a glass or two of unidentifiable

beverages, I had my one and only conversation with a young American lepidopterist, Bob Silberglied. Our paths would surely have crossed many more times if Bob had not died so tragically in the icy waters of the Potomac River just a few months later as a passenger aboard the ill-fated Air Florida Flight 90, but even just that single meeting left a lasting legacy with me. Among the things we discussed was his exciting off-the-wall idea that the then so-called eunuch morph of butterfly sperm might actually have evolved to serve some adaptive function in sperm competition. So when, a few years later, Mark Bellis, who knew a lot more about human sperm than I did at the time, began to describe all the different infertile morphs known to exist in perfectly normal human ejaculates, everything fell into place. It matters not a jot to anybody else, but we would both love to know which of us first suggested: "So maybe these infertile human morphs serve some adaptive purpose too."

Everywhere that Mark and I went, uninhibited conversations would erupt about the evolution of sperm shape, penis shape, testis size, thrusting, masturbation, mucus, orgasm and homosexuality. We must have emptied many a genteel bar and cozy dining room as we hammered out our ideas—and to our list of room-emptiers we eventually added the topic of the "flowback". We had been musing over the female orgasm from the beginning, firmly believing it to be part of the overall story of sperm competition but unable to see how. The stumbling block was our suspicion that the majority of female climaxes had nothing to do with copulation, something for which we later obtained data. So how then could those climaxes have anything to do with sperm competition?

The eventual game-changer was a chance remark by a girlfriend of mine. At the time I was a single parent looking after three young sons but had just met the woman, Elizabeth Oram, who later became the mother of my next three children. Mark and I were well into our work showing that the number and types of sperm that men ejaculate vary exquisitely and apparently adaptively from one occasion to the next. So when Liz said that she couldn't see why such fine adjustments were important when so much of the ejaculate comes back out of the woman within the hour, her remark triggered a whole new series of over-drink conversations. Liz could easily have regretted her comment because soon afterwards she had been press-ganged into pioneering—with more than a little indignity—a technique for the collection of flowback that was standard enough to pass on to other female volunteers. A whole new study had been born which had never been attempted before, has not been repeated since, and may never be allowed again, not least for ethical reasons.

Ethical reasons… Mark and I are fully aware how lucky we were to have started our studies when we did. The 10 years we spent working freely on human sperm competition could not have been more exciting and I would not have swapped them for anything. Each day seemed to bring some new twist, development, or idea. But towards the end of that decade, ethical committee dictate and health-and-safety restrictions driven by the specter of AIDS were beginning to bite. We probably would not have been allowed to continue our work in the cavalier way that suited us anyway, but in the end it did not really matter. We were both beginning to feel it was time to move on to new and different challenges—and we did.

For my part, I had always fantasized about being a full-time writer, particularly a novelist, preferably near the warmer shores of the Mediterranean, and in 1996, it seemed that there would never be a better moment to make the leap. It did not mean that my fascination with the Evolution of Sexuality had lessened in any sense, just that I could now explore new ways to indulge that fascination. As for Mark… He rapidly became a Professor and Director of the Centre for Public Health at John Moores University, Liverpool. Then in 2009, he was awarded an Order of the British Empire (OBE) for services to Healthcare, and in 2013 moved into politics as Director of the Policy, Research and Development division of Public Health in Wales; another successful protégé, another real buzz.

To an extent, while Mark and I were active participants the study of human sperm competition was nestling somewhere within biology, medicine, anthropology, and psychology. Our invitations to lecture came from all of these disciplines, and we were never quite sure how to describe ourselves and our approach. But on our departure, the subject moved quickly into the single arena of evolutionary psychology. Early workers such as Randy Hepburn and Dev Singh found ingenious new ways to study the subject without actually collecting sperm, and in recent years, this approach has been hugely and successfully expanded in all sorts of ways by Todd Shackelford and the team he has assembled, though I am thrilled to hear that he is now collecting sperm as well.

Human sperm competition is still as exciting a field for me as it ever was—but it is only one small part of the mushrooming whole that is the modern discipline of the Evolution of Sexuality. If somebody had shown me the Table of Contents from this volume during my undergraduate years early in the 1960s when Geoff and I were daily having to justify the study of the evolution of any form of behavior as a valid subject… If somebody had told me that these were the things respected scientists would be discussing 50 years into the future… I would have been totally incredulous, and incredibly excited. It really would all have seemed a brilliant dream. But…

Would I actually trade all my buzz-moments from the narrow pioneering past for those being generated across such a wide and fascinating range of subject areas in this field now?

That's a tough one.

January 2014   Robin Baker

Preface

In March 2013, we welcomed dozens of scholars from the USA and Europe to join us at Oakland University in Rochester, Michigan, for a day-long interdisciplinary conference on "The Evolution of Sexuality." We invited as panelists some of the leading scholars in sexual science from many different disciplines, including psychology, criminology, biology, anthropology, archeology, law, philosophy, and medicine. Each of these scholars had conducted and published substantial work addressing sexuality from an evolutionary perspective. This volume showcases the groundbreaking empirical and theoretical work from several of these panelists and other distinguished conference guests.

Biologist Robin Baker provides a thoughtful Foreword to the volume, in many ways setting the stage for the remaining chapters. The first five chapters present summaries of research on the evolution of sexuality from several different disciplinary perspectives. In the first chapter, biologist Tracey Chapman presents a masterful review of sexual conflict. The potential for sexual conflict is pervasive, especially in outbreeding, nonmonogamous species. Sexual conflict results from divergence between the sexes over reproductive resources. Chapman's focus is on our current understanding of sexual conflict from the perspective of evolutionary biology, and she draws skillfully upon studies across diverse species. Chapman reviews a rich literature demonstrating that sexual conflict can occur over a range of different reproductive traits and behaviors, from who to mate with, to how much parental care to give. The intensity of sexual conflict over the level of expression of a reproductive trait or behavior has been assessed by measuring its costs and benefits, in terms of reproductive output, for individuals of each sex. Chapman argues persuasively that outcomes of sexual interactions between males and females can be viewed in terms of Hamilton's quartet of social behaviors: mutual benefit (co-operation), selfishness, altruism, and spite. Chapman showcases recent work that has focused on the mechanisms used by individuals to calibrate their responses to perceived threat levels from sexual competitors.

Literary scholar Judith Saunders presents an overview of the new field called "Darwinian literary analysis", which she helped to create. In a wonderfully original contribution, Saunders applies an evolutionary lens to sexuality in literatures of the past and present, showcasing the value of Darwin's insights for securing a richer

appreciation of core themes and characters in literature. Next, anthropologist Henry Harpending and polymath Gregory Cochran develop a quantitative genetic model of positive assortative mating for a neutral trait. Harpending and Cochran argue that even though a trait is selectively neutral, the mating system can mimic strong selection both for and against that trait, depending on the group membership of an individual. As a consequence, the mating system can generate large group differences rapidly, and if the system persists, arbitrary groups can be transformed into hereditary castes.

In their chapter, psychologists Yael Sela and her colleagues review recent research investigating whether oral sex might function as "mate retention." Men and women perform mate retention behaviors to reduce the likelihood of their long-term partner's infidelity. One mate retention strategy used by both sexes is to increase their partner's relationship satisfaction by provisioning her or him with benefits. Sela and colleagues review recent work indicating that men who report performing more mate retention behaviors, in general, and more benefit-provisioning mate retention behaviors, in particular, also report greater interest in, and more time spent, performing oral sex on their female partner. Likewise, women who report performing more benefit-provisioning mate retention behaviors also report greater interest in, and more time spent, performing oral sex on their male partner—but this relationship is stronger for men. Sela and colleagues highlight sex similarities and differences, discuss explanations for the results, address limitations of this research, and suggest future directions for research investigating oral sex as a mate retention behavior.

Anthropologist and historian Laura Betzig opens her chapter with reference to a cold day in January of 1649 when, after 7 years of wars, the king of England was taken to Whitehall Palace and beheaded. In the months that followed, the parliament passed an Act Abolishing the Office of King, an Act Abolishing the House of Peers, and an Act Declaring England to be a Commonwealth. As Betzig recounts, arguments have been presented that the English Revolution was caused by the rise of Puritanism, the rise of the middle class, and the difficulty of fighting domestic wars on three fronts. Betzig presents a compelling argument in this chapter for another cause. Betzig argues that Charles I was executed—and his son eventually restored—because his wife was the daughter of a king of France. According to Betzig, Queens of England had always struggled on behalf of their sons. Betzig's thesis is that this war was an effect, at least partly, of parent-offspring conflict.

The next three chapters present summaries of different areas of recent research investigating female sexual psychology and behavior. First, psychologist James Roney reviews evidence for the functional roles of hormonal signals in the regulation of women's sexual motivation. Hormone production fluctuates over time with events leading up to and following ovulation, and evolved mechanisms can use circulating hormone concentrations as information about current reproductive states. Roney reviews work documenting that, in most mammalian females, current fecundity is positively signaled by the combination of high estrogen and low progesterone. According to Roney, given the costs of sexual behavior, we might predict that sexual motivation will be higher when fecundity is higher. And in fact, estradiol

positively predicts female sexual motivation across a wide range of mammals, whereas progesterone negatively predicts female sexual motivation. If women's sexual motivation is similarly calibrated to fluctuations in fecundity, Roney argues, we can likewise expect women's libido to be positively and negatively predicted by fluctuations in estradiol and progesterone, respectively. Roney reviews some of the fascinating results from a recent study conducted in his lab which demonstrated that estradiol concentrations were, in fact, positive predictors of within-cycle fluctuations in women's daily reports of sexual desire, whereas progesterone concentrations were strongly negative predictors. Roney concludes the chapter by arguing that these findings suggest that phylogenetically conserved brain mechanisms use hormonal signals to partially calibrate women's sexual motivation to fluctuations in fecundity.

The difficulty of inducing orgasm in women, the variability of orgasm between women, and the lack of an established relationship of orgasm with conception have led some researchers to conclude that female orgasm is a nonfunctional byproduct of male orgasm. As anthropologists John Wheatley and David Puts argue in their chapter, however, other researchers have presented evidence that orgasm is an adaptation in women. Wheatley and Puts review the evidence for these opposing hypotheses and present a convincing argument in favor of the adaptationist hypothesis. First, the authors discuss the phenomenological, anatomical, and neurological correlates of women's orgasm, which are inconsistent with the hypothesis that female orgasm is a byproduct. Wheatley and Puts then present powerful evidence that female orgasm enhances the likelihood of conception, and they summarize evidence that female orgasm functions as a mechanism for choosing mates of high genetic quality, investment potential, or both.

Biologist Randy Thornhill and psychologist Steve Gangestad address the functional design and phylogeny of women's sexuality. Thornhill and Gangestad note that in the past two decades, substantial research has documented estrus in women. Estrus in women is accompanied by a suite of sexual preferences, manifested in the fertile phase of the menstrual cycle, for partners with traits that indicate male genetic and phenotypic quality. Thornhill and Gangestad hypothesize that women's estrus is an adaptation to obtain genes, including conditionally via extra-pair copulation, that enhance the reproductive value of resulting offspring. The authors present a compelling argument that women's estrus is ancient phylogenetically, and has homology and functional similarity with estrus throughout vertebrates. Women's sexuality at infertile cycle points and other infertile times is referred to as "extended sexuality." As Thornhill and Gangestad note, extended sexuality is common in Old World primates and may also be common in pair-bonding, socially monogamous birds. According to the authors, the kinds of preferences associated with women's extended sexuality corroborate the hypothesis that its function is to obtain nongenetic material benefits and services from men in exchange for granting sexual access. Concealed estrus is present in women as evidenced by men's limited ability (compared to other male mammals) to detect estrus, women's limited behavioral changes (compared to other female mammals) during estrus, and estrous women's efforts to limit male mate guarding. The authors conclude the chapter with a superb

review and discussion of concealed estrus in women, marshalling evidence to support the hypothesis that concealed estrus functions in extra-pair copulation to cuckold a regular partner in service of better genes for offspring, while maintaining a regular partner's material benefits.

The next two chapters provide reviews of recent empirical and theoretical work on the evolution of male sexual psychology and behavior, with a focus on homosexual psychology and behavior. Psychologists Paul Vasey and Doug VanderLaan address transgendered male androphilia in the human ancestral environment. *Androphilia* refers to predominant sexual attraction and arousal to adult males, whereas *gynephilia* refers to predominant sexual attraction and arousal to adult females. According to Vasey and VanderLaan, the manner in which male androphilia is expressed varies cross-culturally. *Sex-gender congruent male androphiles* occupy the gender role typical of their sex, behave in a relatively masculine manner, and identify as "men." In contrast, *transgendered male androphiles* often behave in a highly effeminate manner and identify as neither "men," nor "women." Instead, they often identify as members of a third gender. The authors review work indicating that, despite exhibiting different gender role presentations and gender identities, both forms of male androphilia are characterized by the same biodemographic and developmental correlates, indicating that they share a common etiological basis. As discussed by Vasey and VanderLaan, male androphilia presents an evolutionary paradox because it appears to have a genetic component, yet it compromises reproduction and archaeological evidence suggests that it has persisted for many thousands of years. Vasey and VanderLaan argue that the ancestral form of male androphilia was the transgendered form. The authors review some of their own stunningly creative research on a population of transgendered male androphiles in Samoa designed to test hypotheses addressing the evolution of male androphilia. The results of this research indicate that the mothers, paternal grandmothers and maternal grandmothers of *fa'afafine* produce more offspring than those of male gynephiles, which is consistent with the Sexually Antagonistic Gene hypothesis. The results of this research also indicate that *fa'afafine* display elevated avuncular tendencies and behavior compared to women and gynephilic men, which is consistent with the Kin Selection Hypothesis. Vasey and VanderLaan also highlight the results of recent research indicating that the *fa'afafine's* avuncular cognition displays elements of adaptive design.

All else equal, men who are less interested in having reproductive sex will produce fewer offspring and thus selection will eliminate the genes that contribute to their sexual orientation. However, according to psychologist Austin Jeffery, all else is not equal, as sexual orientation corresponds with a constellation of traits that may inform reproductive success. Jeffery presents two original hypotheses regarding the adaptive logic of reduced interest in the opposite sex. The first hypothesis addresses the tradeoff between offspring quantity and quality, proposing that men who abstain from sex with women make more effective parents. The second hypothesis invokes sperm competition and suggests that sneak copulating men can benefit from reduced arousal towards women. The question of exclusive homosexuality is addressed in the final section. Jeffery contends that self-identification as an

exclusive homosexual is the product of a culture that promotes exclusive sexualities to isolate and remove non-heterosexuals from the reproductive arena. According to Jeffery, "coming out" as a homosexual man serves to distinguish oneself as a non-competitor to local sexual rivals, alleviating the severity of one's victimization at their hands. Jeffery argues that the modern notion of sexual identity has corrupted our understanding of sexuality as a fluid and functional product of evolved cognitive mechanisms. According to Jeffery, reliance on categorical sexual archetypes subverts our ability to characterize sexual variance, not only by limiting the depth of our measures, but also by limiting the depth of our theoretical thinking.

The final two chapters are broad in scope, addressing the evolution of both female and male sexual psychology and behavior. Psychologist David Schmitt opens his wide-ranging chapter noting that psychologists have identified myriad ways men and women differ in emotion, behavior, and cognition. Social role theorists assume that men's and women's psychological differences are the result exclusively of sex role socialization processes and sociopolitical power differentials. These theorists assume psychological sex differences will be smaller in cultures with more egalitarian sex role socialization and greater sociopolitical gender equity. In this chapter, Schmitt presents evidence across 21 data sources that directly challenges this assumption of social role theory. Schmitt reports that sex differences in most psychological traits—and even in many physical traits, including height, obesity, and blood pressure—are much larger in cultures with more egalitarian sex role socialization and greater sociopolitical gender equity. Schmitt argues that three alternative evolutionary perspectives on psychological sex differences—obligate sex differences, facultatively mediated sex differences, and emergently moderated sex differences—better explain the universal and culturally variable sex differences reliably observed across human cultures.

In the final chapter, psychologists Michael Pham and Todd Shackelford begin with a brief introduction to sperm competition theory. Sperm competition occurs when a female copulates with two or more males within a sufficiently brief time period, resulting in sperm of the different males competing to fertilize ova. Sperm competition has been documented or inferred to occur in many species. Pham and Shackelford review the evidence for sperm competition in humans. Specifically, the authors review literature indicating apparently convergent adaptations to sperm competition in humans and nonhumans. Pham and Shackelford discuss future research directions, and conclude that the research that documents anatomical, biological, physiological, and behavioral adaptations to human sperm competition provides compelling evidence that sperm competition has been a recurrent feature of human evolutionary history.

The Evolution of Sexuality showcases the profound and wide-ranging intellectual value of an interdisciplinary approach to human psychology and behavior. Guided by Darwin's insights, the contributions to this volume provide a compelling case for an evolutionary analysis of sexuality.

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Chapter 1
Sexual Conflict and Evolutionary Psychology: Towards a Unified Framework

Tracey Chapman

Sexual Conflict: What Is It, Why Does It Occur, How Do We Measure It, and Why Does It Matter?

It was realized, particularly in the 1970s, that rather than being cooperative ventures, the interactions between the sexes over reproduction are often characterized by conflict rather than cooperation (Parker 1979; Trivers 1972). Therefore, as well as the exquisitely coordinated and spectacular courtship displays of birds (Krebs and Davies 1987), reproductive contests can result in mortal injury to females, the evolution of female-damaging penile spines, and female lifespan-shortening seminal fluids (Chapman et al. 2003a). A gene-centered perspective (Dawkins 1976; Hamilton 1964; Parker 1979; Trivers 1972) explains these seemingly paradoxical phenomena, which are central features of sexual conflict.

The underlying reason for sexual conflict is that males and females often "disagree" about how much energy and resources to invest in each reproductive bout and how often to make that investment. For example, males of many species often gain more fitness from mating frequently than do females (Bateman 1948). This is partly because the costs of each mating are often higher for females than males (Bell and Koufopanou 1986; Chapman et al. 2003a; Partridge and Harvey 1988; Partridge and Hurst 1998). Because mating frequency is an emergent property of the interaction of both sexes, it can only take one value—therefore the different interests of males and females cannot simultaneously be realized (Holland and Rice 1998; Parker 1979, 2006; Partridge and Hurst 1998). In any situation in which this kind of evolutionary tension exists, there is the potential for sexual conflict (Fig. 1.1). Therefore, although reproduction often requires some cooperation to succeed, there are many situations in which one sex can gain fitness (i.e., increased transmission of genes) if they can cause their partner to increase reproductive investment (Krebs and Davies 1987). The strategy by which one sex manipulates the other to increase

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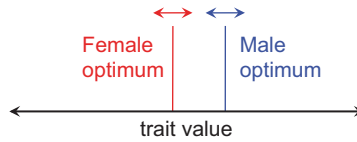e-mail: tracey.chapman@uea.ac.uk

Fig. 1.1 A summary of the basis of sexual conflict. The optimum value of a reproductive trait (trait value) that maximizes male or female lifetime fitness (the number of offspring they produce over their lifetimes) is often different. The sexual conflict that arises from such differences is predicted to be particularly strong when unrelated individuals reproduce and when the mating system is nonmonogamous. These factors reduce the shared interest of each sex in what happens to the other in the future. Therefore, selection to maximize the investment of the other sex in the current reproductive bout at the expense of future costs to the other sex can be selected for. In the example shown here the optimum value of the trait for females is lower than for males. Therefore, a female's lifetime fitness would be higher if the value of the trait were lower. For males, the situation is the opposite. Since the reproductive traits in question are "shared", that is they arise because of an interaction between the sexes (e.g., mating frequency, mating duration, number of eggs laid), the trait can only take one value. Hence, when the trait is expressed at least one sex will not be at its optimum

reproductive investment can be strongly selected even if it results in significant lifetime costs to the manipulated partner. This in turn will select for the manipulated sex to evolve resistance to the manipulation. This creates the evolutionary back and forth that constitutes sexually antagonistic coevolution (Arnqvist and Rowe 2005; Holland and Rice 1998).

Over the last few decades, it has become clear that under any apparent reproductive *status quo*, there is sometimes fast and furious dynamic evolutionary change, driven by adaptation in males followed by counter-adaptation in females (Arnqvist and Rowe 2005). Unless perturbed, this sexually antagonistic coevolution can be difficult to observe at the level of the phenotype, but can productively be investigated via experimentation (Chapman et al. 2003a). Sexually antagonistic coevolution can occur between the same or different loci in males and females (intra- and interlocus sexual conflict, respectively (e.g., Chapman et al. 2003a, and see below) and can generate considerable evolutionary change. Importantly, this coevolution has the potential to lead to reproductive isolation and even speciation (Hayashi et al. 2007; Parker and Partridge 1998; Rice 1998) and is, therefore, of central importance in evolutionary biology.

A huge variety of reproductive traits can be subject to sexually antagonistic selection, from who to mate with, how often to mate, how long to mate, and how much to invest in reproduction (Chapman et al. 2003a). The potential for sexual conflict is universal across all species that engage in sexual reproduction. For instance, it does not even require the existence of separate sexes and can occur over the optimal investment allocated to either male or female sex allocation in hermaphrodites (Charnov 1979). However, whether sexual conflict is realized (Bourke and Franks 1995; Chapman 2006; Ratnieks and Reeve 1992), and the intensity with which it proceeds, depends upon several different factors, as summarized in Table 1.1.

Table 1.1 Factors affecting the expression and intensity of sexual conflict

Factor	Effect on the intensity of sexual conflict
Relatedness	Sexual conflict is exacerbated by low relatedness between reproducing partners (Bourke 2009; Dawkins 1976; Parker 1979, 2006; Rankin 2011). Low relatedness makes it much less likely that currently paired males and females will have a shared evolutionary interest in each other's future
Mating system	Sexual conflict is also exacerbated by nonmonogamous mating systems, as these also promote divergence in the genetic interests of males and females in current versus future offspring. If there is a significant chance of additional reproduction with other partners, then sexual conflict will be increased (Bourke 2009; Dawkins 1976; Parker 1979, 2006; Rankin 2011)
Biologically relevant context	Sexual conflict must be studied in a biologically relevant context. For example, it is difficult to detect patterns of elevated reproduction in populations reproducing at either a low level or at their upper limit (VanderLaan et al. 2012). Nutritional environment can also completely change the direction of sexually antagonistic interactions (Fricke et al. 2009a), so must be considered
Condition	Condition refers to the extent to which individuals can express their genotype, even under poor environmental conditions. It can therefore magnify the differences in quality between individuals (Rowe and Houle 1996) and affect the extent to which they can respond to stimuli. Therefore, condition is likely to alter the intensity of sexual conflict. Variation in condition caused by environmental variation in food availability can alter the extent to which males can express potential sexual conflict adaptations (Amitin and Pitnick 2007; Fricke et al. 2008; McGraw et al. 2007), and also the degree of female responses to them (Fricke et al. 2009a)
Sexual conflict load	Load is the magnitude of the decrease in fitness resulting from each sex not being at its optimum. The larger this difference, the more "distance" required in order to reach the optimum and therefore the stronger the selection arising from sexual conflict
Value of winning	This is the magnitude of the benefit of a sexually antagonistic adaptation in one sex versus the benefits of resisting it in the other, and will determine the strength of sexual conflict
Power	Power refers to the relative costs involved in the value of winning and will thus also determine the strength of sexual conflict
Mechanism	Even if there is the potential for conflict, it may not be manifested if there is no mechanism for each sex to alter the balance of power and winning. This could arise if one sex has effectively "won" the conflict and shut down the opportunities for the other to influence sexual conflict phenotypes (Chapman 2006)
Negative intersexual genetic fitness correlations	Several researchers have found genetic correlations for fitness across generations that vary in direction across sexes. For example, high fitness females may have high fitness sons but average fitness daughters, and vice versa (Chippindale et al. 2001; Foerster et al. 2007). These correlations intensify sexual conflict, because they can constrain the ability of each sex to reach their sex-specific optimum

Concepts and Currency of Sexual Conflict

Costs, Benefits and Fitness

Central to the understanding of sexual conflict is to clarify what is meant by costs and benefits. Though not often explicitly stated, a Hamiltonian (Hamilton 1964) definition is used, such that the outcome of sexual conflict is measured in terms of positive or negative direct fitness consequences for males and females. Direct fitness is defined as that gained through the production of an individual's own offspring. Within a kin-selected context (i.e., within related social groups), sexual conflict is expected to be low (because there are higher shared interests between partners in each other's futures), though it is still possible (Bourke 2009; Parker 1979; Rankin 2011). Some portion of the costs and benefits of sexual conflict can also be measured in terms of indirect fitness (i.e., the portion of fitness gained by helping related individuals to reproduce).

Fitness is a property of a gene, but is often also used with reference to a genotype or individual. This is legitimate in situations where the interests of genes and the individuals in which they reside concur. The currency of sexual conflict is therefore changes in gene frequency, i.e., the basic units of evolutionary change. Conflicts ultimately occur because of differences in how genes maximize their transmission to future generations through males or females. As the interests of genes and the individuals in which they reside are usually (but not inevitably) aligned, it is often convenient to think about sexual conflict in terms of conflicts between individual males and females. We usually use as a proxy for an individual's direct fitness, the number of offspring produced by an individual in their lifetime. This measure may usefully be combined with estimates of survival to give greater weight to offspring produced early in life, when natural selection is strongest (Charlesworth 1980). Fitness is not a property of a group or of a population, as these are seldom units of selection. At a population level, the mean fitness of males and females is equal (Fisher 1930; Arnqvist 2004); instead, it is the relative fitness of individual male and female genotypes that vary.

Measurements of fitness should ideally include a competitive element and a component that can capture the expression of any delayed costs of reproduction (Edward et al. 2011). If the quality of offspring, in addition to the quantity of offspring, is an important component of fitness, then fitness measures necessarily resolve into tests of the effects of the reproductive strategies of parents across generations. In some such studies, the costs experienced by female parents as a result of sexual conflict may be partially compensated for by an increase in offspring quality/fitness (Priest et al. 2008). This has led some researchers to question the sexual conflict paradigm, suggesting that if the costs of sexual conflict are compensated for by genetic benefits to future generations, then there is no conflict. However, it is clear from several studies that the magnitude of direct current costs to parents often exceeds any future indirect genetic benefits to offspring (e.g., Brommer et al. 2012; Lew et al. 2006), hence sexual conflict is the dominant source of selection. The key point is that, through careful measurements of costs and benefits and consideration of the factors summarized in Table 1.1, it is possible to predict the extent and importance of sexual conflict (Fricke et al. 2009b).

Intra- Versus Interlocus Sexual Conflict

The theory and mechanisms of sexual conflict are often cast in terms of whether the conflict is mediated by the same or different loci in males and females (Holland and Rice 1998). This is not purely a semantic categorization—differences in these underlying modes can determine the evolutionary outcome of conflict. Apart from the presence of the Y (or equivalent) sex chromosome in individuals of the heterogametic sex, each cell of an individual carries a full set of all genes in the genome. However, genes can exhibit complex patterns of tissue-, life history stage-, and sex-specific expression. For example, seminal fluid protein-encoding genes are switched on in the reproductive system of sexually mature adult males, but not in females. Genes can also exhibit sex-biased expression, particularly for reproductive genes, i.e., they are expressed at a significantly higher level in one sex in comparison to the other (Civetta and Singh 1999; Ellegren and Parsch 2007; Parisi et al. 2004). Different alleles of the same gene can have different expression levels, or expression levels of the same allele can be regulated differently in males and females. The nature and outcomes of the two major modes of sexual conflict are described below.

Intralocus Sexual Conflict A well-supported example from invertebrates is that of adult locomotory activity in the fruitfly *Drosophila melanogaster*. The positive genetic correlation between movement levels in males and females suggests that the same genes influence adult locomotion in both sexes. However, there is sexual conflict—a high level of activity is beneficial to males as it increases female encounters, leading to increased reproductive success. In contrast, females who are less active have higher fitness, because they have more time available for feeding and egg laying (Long and Rice 2007). Further evidence for intralocus sexual conflict has been gleaned from experiments conducted in fruitflies using ingenious cytogenetic techniques (Chippindale et al. 2001). In these experiments, the same genome can be expressed in males or females and the fitness consequences then measured. These experiments show that there is little fitness difference during larval development (where sexual conflict in minimal), but that at the adult stage, genomes that confer high fitness for males result in low fitness when expressed in females, and vice versa. In addition, experimental evolution experiments have, by various techniques, allowed the genomes of either males or females to evolve free of the constraint of passage through the other sex (Holland and Rice 1999; Rice 1992, 1996). This invariably results in the evolution of a genome that is "better suited" to either male or female interests. The outcome of these intralocus sexual conflicts is predicted to be an evolutionary to and fro depending on whether specific alleles currently reside in males or females (Hayashi et al. 2007; Parker 1979). Resolution of this sexual conflict is also predicted to occur via the evolution of sex limitation, i.e., the silencing of expression of the gene subject to conflict in one sex but not the other. However, this is not necessarily the end of sexual conflict (Chapman et al. 2003a; Chapman 2006).

Interlocus sexual conflict can occur when reproductive traits are influenced by different genes in each sex (e.g., mating frequency; Arnqvist and Rowe 2005).

There is a huge volume of evidence for sexual conflict under this mode (Arnqvist and Rowe 2005), provided by the economic studies of costs and benefits for males and females of manipulating the trait values up and down. A revealing example comes from studies in pondskaters, where the grasping adaptations of males that aid in attachment during mating can be made less effective at achieving matings by experimental manipulation of a specific antigrasping adaptation in females (Arnqvist and Rowe 1995). The predicted evolutionary outcomes of this type of conflict are varied and include evolutionary chases, equilibrium, divergence (Hayashi et al. 2007), or dampening down of the conflict (Arnqvist and Rowe 2005), reflecting a kind of conflict resolution.

Sexual Conflict in Action

The detailed experimental study of sexual conflict has been dominated by studies of just a few species and particularly of invertebrates, notably dungflies (*Scathophaga stercoraria* and *Sepsis cynpisea,* e.g., Martin and Hosken 2003; Parker 1970), fruitflies (*Drosophila melanogaster,* e.g., Chapman et al. 1995; Rice 1996), abalone (*Haliotis* spp, e.g., Clark et al. 2009), and various pondskater species (*Aquarius, Gerris* spp, e.g., Arnqvist and Rowe 2002a, b). Within the vertebrates, important work has been done on Dunnocks (*Prunella modularis,* e.g., Davies 1992) and Red Deer (*Cervus elaphus,* e.g., Foerster et al. 2007). Authors such as Haig (e.g., Haig and Wilczek 2006) have also elegantly outlined the potential for sexual conflict over embryo provisioning in plants, emphasizing the key role of relatedness among the interacting parties in driving conflict not only between the sexes, but also between parents and offspring. These examples of sexual conflict in action have usefully been synthesized in several reviews (e.g., Arnqvist and Rowe 2005; Chapman et al. 2003a). In this section, I use just a few selected examples, some with specific relevance to humans, to illustrate the evolutionary potential of sexual conflict over different reproductive traits in widely different species.

Sexual Conflict over the Effects of Seminal Fluid Proteins in Fruitflies

A valuable model for empirical studies has been the fruitfly *D. melanogaster*, and experimental evolution has been conducted to reveal the covert arms races and evolutionary constraints that accompany sexual conflict (e.g., Rice 1992, 1996). A particular focus of interest has been the actions of the seminal fluid proteins, the nonsperm components of the male ejaculate (Chapman 2001; Ram and Wolfner 2007; Sirot et al. 2014; Wolfner 2002). There are over 100 such proteins and peptides in the *D. melanogaster* male, and they are an extraordinarily diverse group of compounds in terms of structure and function (Mueller et al. 2004, 2005). They can

alter female sexual receptivity, ovulation, egg laying, reproductive tract morphology, immunity, feeding behavior, nutrient balancing, sleep patterns, water retention, and lifespan (e.g., Adams and Wolfner 2007; Carvahlo et al 2006; Chapman et al. 2003b; Cognigni et al. 2011; Isaac et al. 2009; Kubli 2003; Liu and Kubli 2003; Peng et al. 2005; Ram and Wolfner 2007; Ribeiro and Dickson 2010; Sirot et al. 2014). Sexual conflict over each of these traits is possible (Sirot et al. 2014).

The genes that encode seminal fluid proteins are among the fastest-evolving (Swanson et al. 2001b). Due to their rapid evolutionary change, there are seminal fluid protein genes that are not found even among close relatives (Wagstaff and Begun 2005a, b; Wong et al. 2008). Though less is known about the seminal fluid proteins of other invertebrates and vertebrates, they appear to be similarly complex (Sirot et al. 2014). Several core seminal fluid functions are maintained across widely different species, even though the genes that encode individual components can be very divergent. These core functional types include: proteases, protease inhibitors, lipases, lectins, cross-linking transaminases, and cysteine rich secretory proteins (CRISPs; e.g., Mueller et al. 2004, 2005; Ram and Wolfner 2007). This finding shows that there can be conservation at the functional, but not genomic, level. The implication is that the lack of genomic conservation might be due, in part, to sexual conflict (Chapman 2001; Clark et al. 2009; Swanson et al. 2001b).

It was discovered some years ago that the transfer of seminal fluid proteins from male to female *D. melanogaster* during mating can decrease female lifespan and reproductive success (Chapman et al. 1995) without any demonstrable benefits for females (e.g., Brommer et al. 2012). Later work identified some of the seminal fluid protein candidates apparently responsible. One example is the 36 amino acid "sex peptide," whose transfer can increase the fitness of males, but decrease that of females that receive it (Fricke et al. 2009c; Wigby and Chapman 2005). The phenotypic effects of sex peptide include decreased female receptivity, increased egg production (Chapman et al. 2003b; Chen et al. 1988; Liu and Kubli 2003), altered female immunity (Domanitskaya et al. 2007; Peng et al. 2005), decreased sleep (Isaac et al. 2009), increased feeding (Carvahlo et al. 2006), and altered nutrient balancing (Ribeiro and Dickson 2010). These findings suggest that the transfer of elevated levels of sex peptide shifts the value of remating and investment into the current batch of eggs towards the male optimum and away from that of the female, with attendant lifespan costs for females. This is consistent with the operation of interlocus sexual conflict. Genome-wide studies of gene expression show that receipt of sex peptide by females causes a change in the expression of many different functional categories of genes, with tissue- and time-specific signatures (Gioti et al. 2012). This suggests that females have many obstacles to overcome to evolve resistance to sex peptide. Other studies indicating toxicity of seminal fluid proteins employed a technique in which seminal fluid proteins were ectopically expressed in females. Four seminal fluid proteins, including sex peptide, were found to decrease female lifespan when expressed in this way (Mueller et al. 2007).

This sexual conflict should select for counter-adaptations in females. However, as yet, we have little understanding of how females respond to the sexually antagonistic effects of male seminal fluid proteins (Wigby and Chapman 2004). Only one

receptor to a seminal fluid protein in insects has been identified (Yapici et al. 2008). Hence, the study of the coevolution of interacting molecules in males and females is only just beginning (Clark et al. 2009). That said, there is good evidence for selectable genetic variation in females for the evolution of resistance to the costly effects of male seminal fluid proteins. For instance, females subjected to elevated levels of sexual conflict over evolutionary time evolved to live longer in the presence of males than did controls (Wigby and Chapman 2004). The fact that the longevity differences were not an intrinsic property of the lines and were not observed in the absence of exposure to males suggests that this was a specific response to the manipulation of sexual conflict levels.

Sexual Conflict over Sperm Egg Interactions in Marine Invertebrates

Abalone are a group of marine invertebrates that broadcast their gametes into the water column. In these species, there is good evidence for antagonistic coevolution between male sperm lysin and its female receptor, vitelline envelope receptor for lysin (VERL) (e.g., Clark et al. 2009; Lee et al. 1995; Metz and Palumbi 1996; Swanson et al. 2001a). Lysin is involved in breaking down the vitelline envelope surrounding the egg and permitting further transit of the sperm to effect fertilization. There is evidence for sexual conflict between the male's efforts to have the sperm enter the egg quickly and the female's efforts to avoid costly polyspermy (Frank 2000). The latter refers to the situation in which too many sperm enter the egg, with lethal results. The dynamic pattern of coevolution between VERL and lysin appears to have resulted in divergence in the VERL receptors in females (Clark et al. 2009; Swanson et al. 2001a). This pattern of evolutionary change is a specific prediction of sexual conflict theory (Hayashi et al. 2007) and is therefore strong evidence for sexual conflict in action.

Sexual Conflict over Mating Frequency in Pondskaters and Beetles

A powerful system for demonstrating the existence of sexual conflict is found in the pondskaters (Arnqvist and Rowe 1995, 2002a, b). Experiments show that lengthening of the female's antigrasping spines reduce the length and success of mating attempts, which is consistent with the evolution of antigrasping spines as defenses against male grasping adaptations (Arnqvist and Rowe 1995). A set of species comparisons was also conducted (Arnqvist and Rowe 2002a, b) in which the relative levels of male grasping and female antigrasping armaments were measured. Interestingly, these adaptations were well "matched" across different species in terms of the absolute size of the male graspers versus the female antigraspers.

However, when there were changes in the relative levels of armament and defense between males and females, there were predictable effects on mating rate. For example, when females had relatively lower levels of defense, mating rate was higher, and vice versa. These studies demonstrate the underlying evolutionary tensions in sexual conflict.

Coevolution driven by sexual conflict is also found in a comparative study of *Callosobruchus* seed beetles (Rönn et al. 2007). In these species, there is a predicted sexual conflict over male mating frequency. Penile spines are proposed to anchor the male during mating, but they also damage the female reproductive tract. Counter-adaptation in females is represented by the evolution of a thicker lining in the reproductive tract. The number of spines and amount of damage was found to vary across the different seed beetle species tested, and a combined measure of the degree of harmfulness of male genitalia (based on number, morphology, and distribution of spines) was correlated with the thickness of the female reproductive tract wall. As in pondskaters, the absolute armament level was independent of the degree of damage. It varied instead with the relative armament level, i.e. harm was more evident in species in which the male genitalia were relatively more spiny and where the female tract was relatively less robust. These findings fit the sexual conflict framework well.

Sexual Conflict over Ovulation in Invertebrates and in Humans

Conflicts between the evolutionary interests of males and females can also diverge with respect to different facets of ovulation, some of which have particular relevance to humans. Some evidence consistent with the sexual conflict over ovulation and the efficiency of egg fertilization has been revealed in *D. melanogaster* fruit-flies. For example, there can be a break down in the efficiency of egg fertilization in matings between normal females and mutant males that lack a seminal fluid protein (Acp26Aa) that stimulates ovulation (Chapman et al. 2001). In invertebrates, ovulation can occur in response to mating or can be enhanced by signals in the ejaculate transferred during mating (Sirot et al. 2014). However, in mammals, ovulation can often be divorced from mating and the receipt of an ejaculate, and influenced instead by seasonal or cyclical factors. A different aspect of ovulation over which there can be sexual conflict is therefore whether it is concealed or unpredictable. This is of particular interest in humans, in which ovulation is thought to be concealed, it is suggested, in order to reinforce pair bonds, increase male parental care, or to reduce the intensity of male–male competition (e.g., Alexander and Noonan 1979; Benshoof and Thornhill 1979; Hrdy 1979; Strassmann 1981). Whether ovulation is concealed in humans is still a topic of debate (e.g., Kuukasjärvi et al. 2004; Thornhill and Gangestad 1999). Whatever the answer, it is possible that the evolution of even partial concealment may have been selected partly to reduce the intensity of sexual conflict generated as a side effect of competition between males.